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EXPERIMENTS ON THE INHERITANCE OF THE "PLUS" AND "MINUS" CHARACTERS IN GLOMERELLA CINGULATA

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(WITH ONE FIGURE)

INTRODUCTION

Edgerton (1914) reported the occurrence of two distinct types of cultures in one or more species of *Glomerella* isolated from various hosts. These types he designated as "plus" and "minus," regarding them as "sexual strains." Although the species of fungi concerned were not definitely identified, it appears probable that at least the one isolated from cottonwood and used extensively in Edgerton's work was *Glomerella cingulata* (Stonem.) S. and v. S. Monoascosporic lines of either the "plus" or the "minus" type were capable of producing fertile perithecia in vitro, though most perithecia of minus lines failed to develop mature spores. When a "plus" isolate was grown in plate culture with a "minus" isolate from the same host, fertile perithecia developed in great abundance along a line where the two strains met. Asci containing the full complement of spores were isolated from perithecia produced along the line between the isolates and cultured individually without separating the ascospores. It was found that both the "plus" and "minus" strains were commonly, though not always, produced in the same ascus. This and other evidence led Edgerton to take the view that fertilization occurred when the two strains came together in a plate (cf. Shear and Wood 1913). He pointed out, however, that the process of fertilization had not been fully studied and that it was impossible to explain with certainty the phenomena he had described.

Though more than 25 years have elapsed since Edgerton's valuable pioneer contribution, and great advances have been made in the field of genetics of fungi, it is still uncertain whether genetic combinations occur between the "plus" and "minus" strains of *G. cingulata*.

In working with a culture of *G. cingulata* from rotted apple, the writer obtained monoascosporic isolates that seem to correspond to Edgerton's plus and minus types. In December, 1939, when the eight spores of an ascus were

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cultured separately, it was observed that four lines were of the "plus" type and four "minus." Experiments were then initiated to study comparatively in pedigreed cultures the incidence of "plus" and "minus" lines in asci arising in monoascosporic "plus" and "minus" clones, respectively, and in asci obtained from perithecia on the line between "plus" and "minus" isolates. This work was unavoidably interrupted in March, 1941, when the writer was called into military service. Though it is hoped that the investigation may be resumed later, it seems more advisable to give the following brief report of the available results than to await the possibility of making a more complete report after further investigation.

MATERIALS AND METHODS

The original culture on which the greater part of the present work has been based was obtained from a bitter rot lesion on a Black Ben Davis apple from Tennessee. Reinoculations into apples incited the characteristic rot in all cases. Another culture that was used to a very limited extent was obtained from Miss A. J. Watson, who had isolated it from a specimen of *Celastrus scandens* L. secured in New Hampshire. The two races represented were designated southern and northern respectively.

Various media were used to culture the fungus. It was found that potato dextrose agar served quite well for the production of conidia and ascospores, and this was selected as the standard medium for the work. The agar was unwashed and the commonly used formula was employed. Varying the pH and the relative carbon content, within limits, affected the rate of growth of the fungus but not the production of either ascospores or conidia. Oat agar, sometimes recommended for use in the production of perithecia, gave no apparent increase in this case. Monosporic isolations were made by means of glass needles used with a stereoscopic binocular microscope. In most cases the spores were removed without regard to their relative position in the ascus.

TYPES OF ISOLATES OBTAINED

Two general types of cultures, designated as light and dark,[1] were obtained. The color differentiation was definite in all cultures and together with other characteristics readily served to distinguish the two types.

The light type is characterized by an abundance of light-colored aerial mycelium. Conidia are produced sparingly but occasionally acervuli are formed which produce pink spore-masses. In the course of a few days cultures of this type produce perithecia which contain fully developed normal asci with viable ascospores. These perithecia are in groups and do not occur distributed throughout the culture like those of the dark type.

[1] Since it is not definitely known whether these types actually enter into genetic combinations with each other, they are hereinafter designed as light and dark. They seem to correspond, respectively, to Edgerton's (1914) "plus" and "minus" strains.

The dark type produces very little aerial mycelium, and in the course of a few days appears carbonaceous. It always produces abundant conidia in large masses on the various media employed, the masses of spores at first giving the cultures a salmon-pink surface coloration. Later perithecia are produced in large numbers over the surface and submerged throughout the medium. These perithecia, however, seldom form asci and when asci are produced they are usually abnormal, the spores not germinating readily. It was found that only one in several hundred perithecia formed even imperfect asci.

When the two types are grown together in the same Petri dish there is a distinct line of perithecia at the junction of the colonies. These contain normal asci with the usual complement of ascospores.

DERIVATION AND BEHAVIOR OF CLONES OF THE SOUTHERN RACE

As explained above, the original culture, designated as stock culture No. 1, was isolated from an apple. Two single ascospores picked out at random from this culture yielded the clones from which all the others of this group were derived. One, a dark type, was designated as 1C and the other, a light types, as 1A. These isolates were then grown together in the same dish, and from the line of perithecia that developed where the two met, single asci were picked out and the spores isolated. One set of eight cultures, X2, derived from the ascospores of a single ascus, was retained for further study, all subsequent cultures being derived from this set.

The derivation and types of the clones of the southern race are diagrammatically shown in figure 1. A solid black disk designates a dark type clone, whereas a circle designates a light type. While the ascospores were always isolated in full sets of eight, occasionally some spores failed to germinate; this accounts for the blank spaces where sets of cultures derived from certain asci are represented. Although the dark type strains are designated first, followed by the light in indicating a set, this does not refer to their relative position in the ascus. Sets marked by the letter X were obtained from the line of perithecia developed between two opposite types, whereas those without the X were obtained from clones grown separately.

Unbroken lines trace the descent of isolates from a monoascosporic clone, and grouped columns of sets below the end of such lines are from the same colony. Broken lines show the derivation of sets from perithecia taken from the line between the dark and light isolates. For example, sets X30 to X38 were obtained from the line of perithecia formed by pairing 58(4) and 58(7). Sets grouped by brackets are all from the same perithecium. For example, sets 91 to 100 were from a single perithecium taken from culture 57(5).

The light and dark strains of the southern race were distinctly differentiated in culture, even under widely varied environmental conditions.

Both types remained constant, whether propagated by conidia or mycelium. It is concluded that these types are hereditary rather than modifications induced as responses to environment.

With one exception asci from monosporic clones of the light type yielded

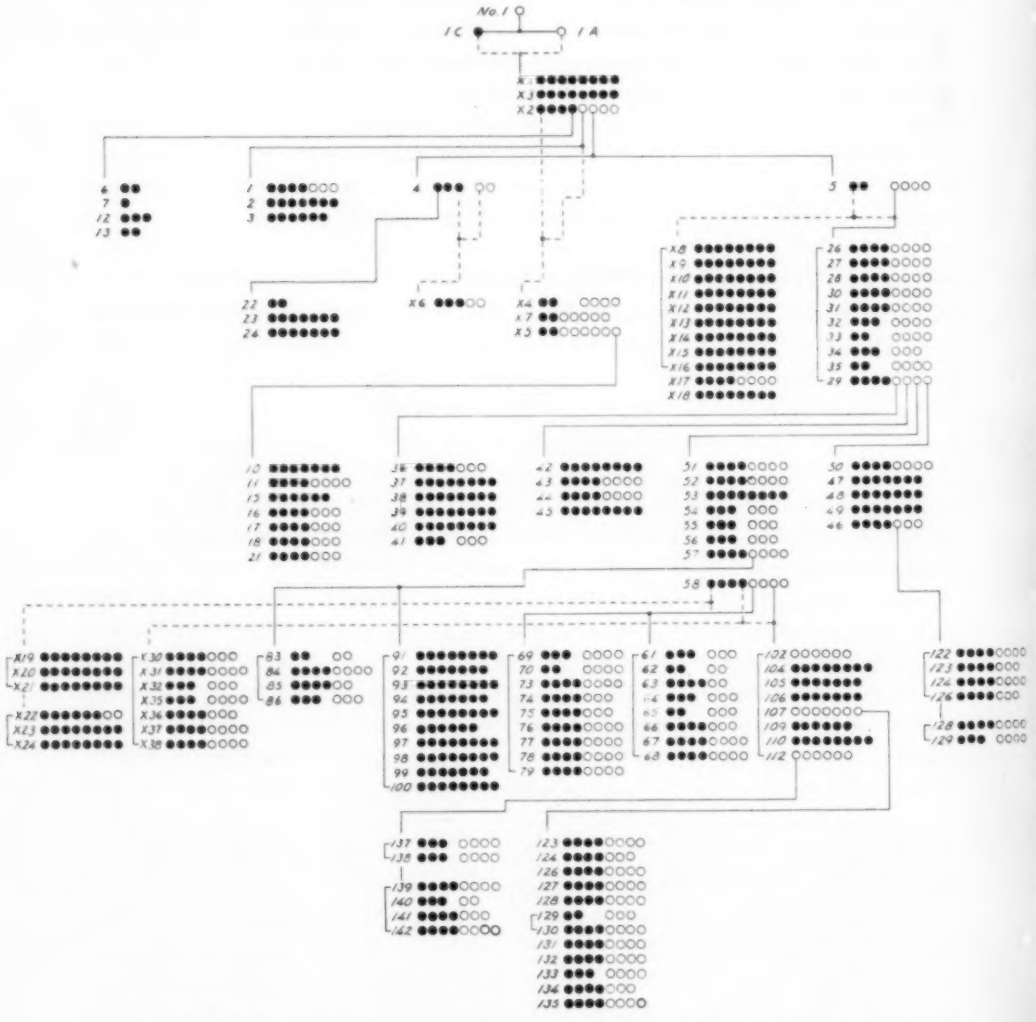

FIG. 1. Derivation and type of the clones of the southern race of *Glomerella cingulata* (see text).

either all dark cultures or four dark and four light. In the exceptional case there were taken from a perithecium of clon 58(7) three asci yielding all light cultures and five asci that gave all dark cultures. When several asci were

taken from a single perithecium they yielded either all dark cultures, or half dark and half light, with the one exception mentioned. In this exceptional case, however, when certain clones from asci that had given all light cultures were studied, for example 107(7) and 112(1), they gave rise to asci yielding dark as well as light strains.

Asci obtained from the dark strain grown alone yielded only dark cultures. The number of isolations is certainly relatively small, because most of the ascospores did not germinate, but as far as the experiment was carried the dark colonies produced nothing but dark offspring.

When asci were taken from perithecia at the junction of dark and light colonies there usually were produced either all dark sets or sets consisting of half dark clones and half light. There were certain instances, however, in which the ratio of the two types in a set was not 1:1, for example: X5 and X7 in which there were 2 dark and the remainder light, and X22 in which there were 6 dark and 2 light. Here again all sets from the same perithecium were alike except X22.

REACTION BETWEEN ISOLATES

Southern race. To determine whether all dark isolates of a set would react to form lines of perithecia when in contact with each light isolate of a set, the clones of certain sets were paired in all possible combinations. When, for instance, the clones of set X2 were so paired it was found that there was a definite line of perithecia where each dark isolate came in contact with each light isolate, but where light isolates came together there was never any such line of perithecia formed, the colonies merely merging. The dark colonies likewise placed together showed no indication of any reaction with one another. In the sets in which there were all light or all dark clones from a single ascus, as for example, 107 and 110, it was found that there were lines of perithecia only between dark and light isolates when the clones of the two sets were placed in all possible combinations.

Northern race. With this culture the clones derived from a single ascus were either all of the dark type or all of the light type. The number examined was small, only 15 asci in all; but this seems to be the normal situation in this race in contrast to that found in the southern race. In pairing the dark and light strains of the northern race, it was found that a line of perithecia was formed only when dark met with light.

Southern race with northern. A southern light strain paired with a northern dark gave a line of perithecia at the junction, and a northern light paired with a southern dark likewise gave perithecia at the meeting line. Southern dark and northern dark gave no line of perithecia, nor did southern light and northern light.

SUMMARY AND CONCLUSIONS

A race of *Glomerella cingulata* (Stonem.) S. and v. S. obtained from a rotted apple from Tennessee was studied for inheritance of light and dark strain characters (apparently corresponding, respectively, to "plus" and "minus" of Edgerton).

Monoascosporic colonies were always either light or dark.

A comparative study was made, using pedigreed cultures, of the incidence of light and dark lines in asci taken, respectively, from monoascosporic light clones, monoascosporic dark clones, and the line of perithecia developed where light and dark strains met in plate culture. Monoascosporic light clones gave asci that yielded all dark clones or half dark and half light, with the exception of one perithecium in which the asci yielded all dark or all light. Monoascosporic dark clones gave asci that yielded only dark clones. Asci taken from perithecia produced where the light and dark types met usually yielded all dark clones or half dark clones and half light. Several such asci, however, yielded dark and light clones in 3:1 or 1:3 ratio.

In limited experiments with a northern race of the same fungus somewhat different results were obtained.

Perhaps the most noteworthy aspect of the results here reported is the common production of all dark clones or half dark clones and half light from asci originating in monoascosporic light lines of the southern race. Explanation of this remarkable phenomenon of continuous production of dark and light clones in 1:1 or 1:0 ratios from asci of a homothallic haploid line must await the results of further work.

The work was carried on under the direct supervision of Dr. G. W. Keitt, to whom the writer is greatly indebted for suggestions and for help in preparing the manuscript.

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CYTOPHYLETIC ANALYSIS OF ASTRANTHIUM INTEGRIFOLIUM

J. T. BALDWIN, JR.

(WITH FOUR FIGURES)

Astranthium integrifolium (Michx.) Nutt., the western daisy, is more generally known as *Bellis integrifolia* and is then congeneric with the English daisy. According to the manuals, the plant occurs from Kentucky and southwestern Missouri to Texas and blooms from May to July.

Seed of *A. integrifolium* (*Mary Wharton 4329*, University of Michigan Herbarium; near Liberty, Casey County, Kentucky) planted in the University of Michigan Botanical Gardens in January 1940 produced flowering specimens during November 1940 and several subsequent months. One of the plants, drawn by Eduardo Salgado, is shown in figure 1; the

FIG. 1. *Astranthium integrifolium* beginning to flower. × 0.7. FIGS. 2–4. Chromosomes of *Astranthium integrifolium:* $2n = 8$ at metaphase in leaf cell; $n = 4$ at first and second metaphase in pollen mother-cell. × 1400.

basal leaves are still present, and the flowers are maturing. The chromosomes were investigated in aceto-carmine smears of leaves, roots, and anthers: $2n = 8$ (fig. 2), $n = 4$ (figs. 3, 4). This somatic number was also determined for plants sent by Miss Wharton from Big Hill, Madison County, Kentucky, and for plants collected with the aid of H. T. Shacklette and A. M. Harvill of the University of Kentucky from near Nashville, Davidson County, Tennessee, from Cliffton, Woodford County, Kentucky, and from the University of Kentucky Botanic Garden. Meiosis was in process in the Tennessee plants on April 15, 1941: $n = 4$.

Representatives of this species are recommended for use in classes in microtechnique. Mitosis may be readily studied in easily made leaf smears (for method, see Baldwin 1939; Sen 1940); meiotic material is not difficult to get, for the flowers of a head develop differentially over an extended period. The plants normally die after blooming, but, if the stems are cut back, flower production will be prevented and thus a constant supply of young leaves insured.

Negodi (1936), working with plants grown from seed obtained from a European botanic garden and identified by De Candolle's (1826) description, reported *Bellis integrifolia* Michx. to have an n-number of 9 chromosomes; in view of the present study of material from the wild, one judges that Negodi mistook the species. Chromosome numbers have been determined for five other representatives of *Bellis:*

	n-number	$2n$-number	Authority
B. annua L.	9		Negodi 1937a
B. perennis L.	9		Ishikawa 1911
			Winge 1917
			Negodi 1937a
		18	Heitz 1926
B. rotundifolia Boiss. & Reut.	9		Negodi 1937b
B. mexicana A. Gray	18		Negodi 1937b
B. sylvestris Cyrill.	18		Negodi 1937a
		54	Tischler 1936

Steyermark (1940) recognized the validity of Nuttall's monotypic *Astranthium.* Chromosome numbers give an additional basis for this generic separation: *A. integrifolium* has an n-number of 4; the six investigated *Bellis* species, n-numbers of 9, 18, or 27. Perhaps *Bellis* (the genus, as listed in *Index Kewensis,* includes about forty species, approximately a third of them being native to the new world) is an amphidiploid result of a union between a 4-chromosome system, of which *Astranthium* is an expression, and a 5-chromosome system. In this connection, it would be interesting to know the chromosomal situation in *Eclipta* L., for Nuttall (1841), writing of *Astranthium,* said: "This genus appears to be much more allied by the fruit to *Eclipta* than to *Bellis.*"

SUMMARY

Astranthium integrifolium has an *n*-number of 4 chromosomes, a 2*n*-number of 8; *Bellis*, as investigated by other workers, has a basic number of 9: these chromosomal data support the separation of *Astranthium* from *Bellis*.

A. integrifolium is recommended for use by students in microtechnique.

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STRUCTURAL FEATURES OF THE SHOOT APICES OF DIPLOID AND COLCHICINE-INDUCED, TETRAPLOID STRAINS OF VINCA ROSEA L.[1]

G. L. Cross and T. J. Johnson

(WITH TWENTY-FOUR FIGURES)

INTRODUCTION

Vinca rosea (Madagascar periwinkle) is an ornamental plant of considerable importance in the southwestern states (fig. 1). Because of its resistance to drouth and disease, and because it blooms over a relatively long period of time during the summer months, the plant is used extensively in public and private gardens. In an effort to produce new and improved varieties through the induction of polyploidy (Eigsti 1938), Schnell (1940) treated seeds and seedlings of both the red and white varieties of *V. rosea* with various mixtures of colchicine, prepared in water, mineral oil, and lanolin. An assortment of tetraploid and octoploid plants, including a few chimeras, was obtained from this treatment. One especially promising white tetraploid strain appeared, and it is being cultivated experimentally at the

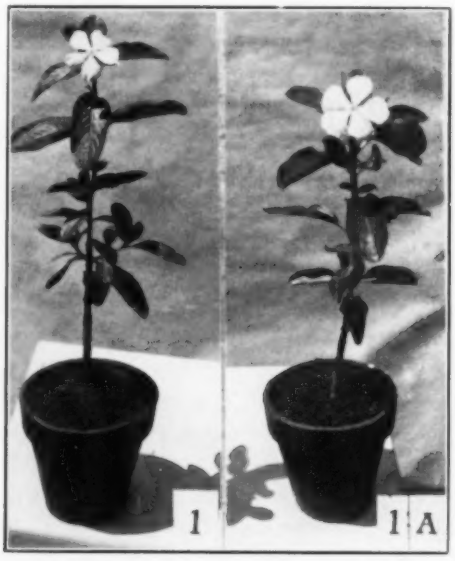


Fig. 1. Diploid plant. Fig. 1A. Tetraploid plant. Note shorter, thicker main axis and heavier, darker leaves. × ⅛.

[1] Contribution from the Botanical Laboratory of the University of Oklahoma, n.s. 66. Publication of the figures was assisted by the Lucien M. Underwood Memorial Fund.

University of Oklahoma. The plants of this new strain have somewhat more massive stems, thicker and greener leaves, and larger flowers (fig. 1A). They grow in height more slowly than the related diploid variety, and frequently are somewhat shorter than diploids of the same age.

Recently Taylor (1941) became interested in the water relations of tetraploid and related diploid varieties of *Vinca*, and his comparative measurements of water absorption and transpiration indicate that the tetraploid strain developed by Schnell may prove to be generally desirable for cultivation in the southwestern part of the United States. The tetraploid strain and several interesting chimeras were given to the present writers for histogenetic studies, and grateful acknowledgment is made to Miss Schnell and Mr. Taylor.

The fundamental importance of apical meristem in problems dealing with growth of the shoot has been stressed recently by Jones (1937), Foster (1939), and Satina, Blakeslee, and Avery (1940). Except for an investigation of colchicine-induced periclinal chimeras of *Datura* (Satina, Blakeslee, and Avery 1940), apparently no comparative studies of the shoot apices of polyploids and related diploids have been made. The present investigation was undertaken in an effort to determine if the changed appearance of colchicine-induced tetraploid periwinkles could be correlated with visible changes in the structure and growth of the apical meristem.

METHODS

The shoot apices used for the present investigation were obtained from white-flowered plants grown from seed in the greenhouses at the University of Oklahoma. The tetraploid material was collected from the F_1 generation of the new strain induced by Schnell (1940). Schnell had treated the apices of two white-flowered plants with a colchicine-lanolin mixture (1:100). After this treatment the main axes died back and lateral, tetraploid branches were developed. Seeds collected from these tetraploid branches produced the F_1 plants here described. Because the flowers of *V. rosea* are normally self-pollinated, it was assumed that the new tetraploid variety would breed true. Such has proved to be the case, as is demonstrated by epidermal characteristics (figs. 2, 2A) and by chromosome counts made from pollen mother cells (figs. 3, 3A)[2] of the F_1.

Tischler (1931) has reported 8 chromosomes for the haploid phase of the normal diploid variety of *V. rosea*, and Simonet and Chopinet (1939) found 16 chromosomes in the corresponding phase of tetraploid varieties. Figures 3 and 3A in the present paper confirm the counts made by these earlier investigators.

[2] Aceto-carmine preparations from which these photographs were made were prepared by Dr. O. J. Eigsti, University of Oklahoma, to whom the writers extend grateful thanks.

The materials were killed and fixed in formalin-acetic-alcohol (5 parts formalin, 7 parts glacial acetic acid, and 88 parts 60 per cent ethyl alcohol) and in Juel's solution (Korody 1937) under reduced pressure. Tertiary butyl alcohol was used for dehydrating and clearing (Cross 1937a), and the materials were embedded in "Tissue Mat." Serial sections were cut 8 μ in thickness; safranin and fast green (Cross 1937a) were used in staining. A

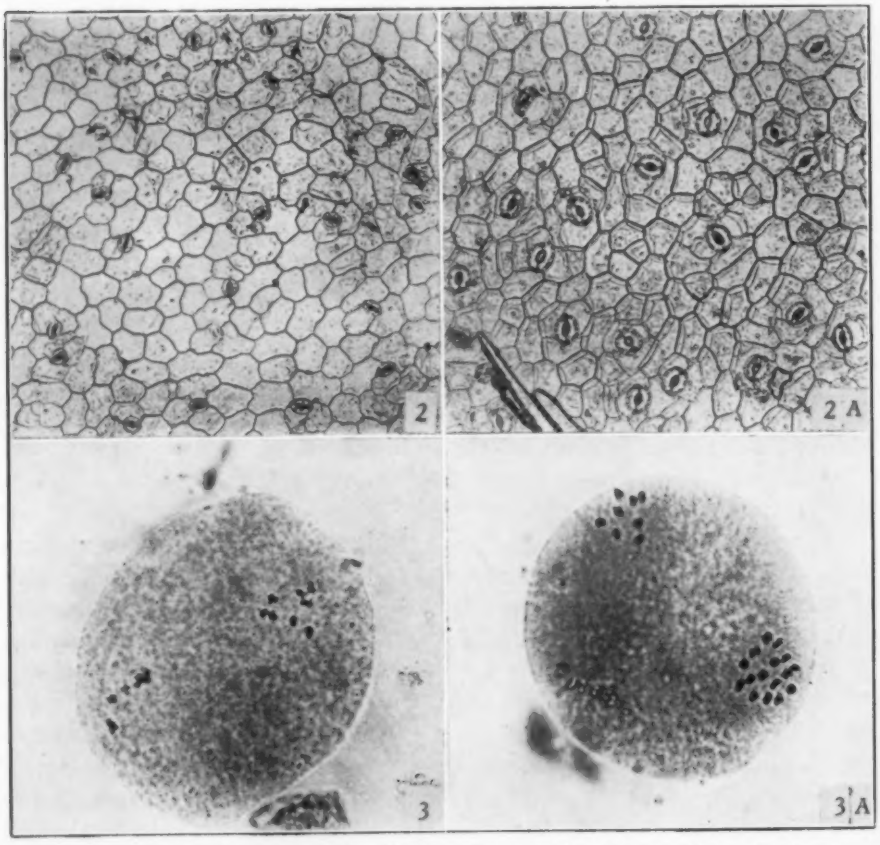


FIG. 2. Diploid epidermis. × 100. FIG. 2A. Tetraploid epidermis. Note that the tetraploid guard cells are considerably larger than the diploid but that the other epidermal cells are about the same size in each strain. × 100. FIG. 3. Diploid microspore mother cell immediately after reduction division, showing chromosomes in groups of 8. × 666. FIG. 3A. Tetraploid microspore mother cell immediately after reduction division, showing chromosomes in groups of 16. × 666.

Wratten A filter, no. 25, was used during photomicrography to emphasize the cell walls.

GENERAL FEATURES OF THE DIPLOID SHOOT

Apparently the only published account of apical meristem in the genus *Vinca* is Schmidt's (1924) description of the shoot apex of *V. minor* L.

In this species there is a three-layered tunica and a central corpus with an irregular cellular pattern. The outer layer of the tunica divides only anticlinally and its derivatives develop into the epidermis of the shoot. The second and third layers of the tunica also divide only anticlinally at the summit of the meristem, but during leaf initiation periclinal divisions occur in the flanks, and the derivatives of these early periclinal divisions produce the internal portions of the leaf. Schmidt was able to demonstate that the derivatives of the second layer of the tunica produce the parenchymatous portions of the leaf, whereas the vascular tissue in this organ is formed from derivatives of the third or innermost layer of the tunica. In the shoot axis derivatives of the tunica produce the epidermal and cortical portions, but the stelar regions, except for the leaf traces, are derived from the corpus. Because the various layers of the tunica and the corpus of *V. minor* make such definite and precise contributions to the shoot axis, Schmidt regarded these growth zones as true histogens equivalent to those of Hanstein (1868) as follows: the first layer of tunica is the dermatogen, the second and third layers of tunica are the periblem, and the corpus is the plerome.

The shoot apex of *V. rosea* is elliptical in transection. The form and size vary during the course of a plastochron—the latter to a greater extent than the former. The "length," "width," and "height" of several apices, in various phases of development between periods of foliar initiation, were measured. As used in this paper the "length" and "width" refer respectively to the long and short axes of elliptical transections immediately above the axils of the youngest leaves. However, the measurements were made from median longitudinal sections. In each apex one dimension ("length" or "width," depending on the plane of the section) was obtained by direct measurement; the other necessarily was obtained by counting sections and multiplying by the thickness of the sections. The "height" was obtained by measuring the vertical distance from the summit to a straight line connecting the axils of the youngest leaves.

Immediately after the initiation of a pair of opposite foliar primordia, when the shoot apex is in a state of minimal surface area, the length of the apical meristem is usually about 70 μ, the width about 45 μ and height from 3 to 5 μ (figs. 4, 10, 15). During the ensuing plastochron the apex gradually increases in size, and attains its maximal surface area just prior to the initiation of the next pair of leaf primordia (figs. 4–10, 15–20). Measurements made at this stage indicate that immediately before leaf initiation the length of the apex is about 160 μ, the width 110 μ, and the height 45–50 μ. However these maximal dimensions are regarded as only approximately correct, because difficulty was experienced in deciding exactly when and between what points measurements should be made. The increased dimensions are attained in a uniform manner—that is, an increase in one dimen-

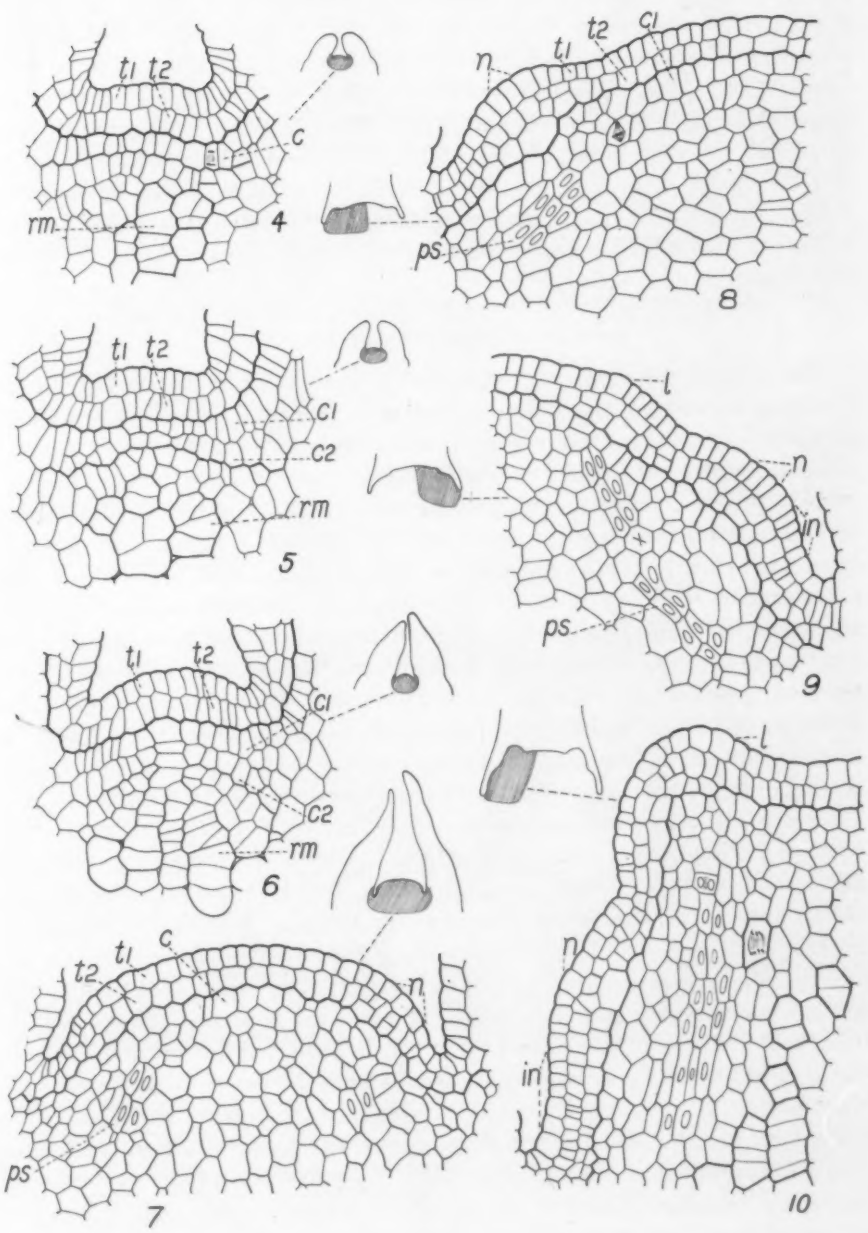
sion is correlated to a certain extent with increases in the others. At the end of each period of enlargement, when the meristem has reached its maximal surface area, a pair of opposite foliar primordia is differentiated in a plane parallel with the long axis of the transectional ellipse, and perpendicular to the plane of the next youngest pair of leaves (figs. 10, 13, 20). At this point it is interesting to note that the range of dimensions given for *V. rosea* is slightly greater than reported by Schmidt for *V. minor* (length 104 μ, width 36 μ, and height 10 μ during minimal surface area, and length 139 μ, width 97 μ, and height 42 μ during maximal surface area).

STRUCTURE OF THE DIPLOID SHOOT APEX DURING MINIMAL SURFACE AREA

Immediately after the initiation of a pair of foliar primordia, median longitudinal sections cut in any plane show that the apex consists of three rather distinct peripheral layers of cells which cap a central region characterized by a somewhat irregular cellular pattern (figs. 4, 15). The two outer layers constitute the tunica. The cells of the tunica divide only anticlinally at the summit of the meristem, but as is shown later, periclinal divisions occur in the flanking portions of the second layer of the tunica during foliar initiation. Frequently a centrally located large cell dominates each of these layers (fig. 18). The third layer at the apex (fig. 4) is the first layer of the corpus. It maintains its identity for a variable period of time after the initiation of foliar primordia, but sooner or later the constituent cells split periclinally (figs. 5, 16) throughout its extent, and often this phenomenon occurs in such a regular manner that four layers of cells may be distinguished at the apex (figs. 6, 17), i.e., two layers of tunica and two of corpus. The layering is remarkably evident immediately beneath the summit,

Explanation of figures 4–10

FIG. 4. Longisection of apical meristem of *V. rosea* in early stage of plastochron, cut parallel with plane of youngest pair of leaves; *t1*, first layer of tunica; *t2*, second layer of tunica; *c*, corpus; *rm*, rib meristem. FIG. 5. Longisection of apical meristem in later stage of plastochron cut in same plane as fig. 4, showing periclinal splitting of cells in first layer of corpus; *c1*, first layer of corpus; *c2*, second layer of corpus. FIG. 6. Longisection of apical meristem cut in same plane as figs. 4 and 5, showing still later stage in plastochron. Note intercellular spaces in rib meristem. FIG. 7. Longisection of apical meristem immediately after foliar initiation, cut perpendicular to plane of youngest pair of leaves; *n*, nodal region; *ps*, provascular tissue. FIG. 8. Longisection of apical meristem cut in same plane as fig. 7, showing later stage in development of nodal region and provascular tissue. Note that provascular tissue is separated from derivatives of the tunica by cells of the corpus. FIG. 9. Longisection of apical meristem showing periclinal divisions in T–2 associated with origin of foliar promordium; *l*, foliar primordium; *n*, nodal region; *in*, internodal region. Note vascular tissue in two youngest internodes separated by undivided cell marked X. FIG. 10. Longisection of apical meristem showing later stage of foliar primordium and further development of nodal and internodal regions. Note acropetal differentiation of provascular tissue. × 325.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but frequently, because of the presence of oblique walls, it may not be seen in the flanking regions of the corpus. For convenience these four layers are hereafter designated as T–1 (first layer of tunica), T–2 (second layer of tunica), C–1 (first layer of corpus), and C–2 (second layer of corpus). A comparison of the description and figures given here for *V. rosea* with those by Schmidt (1924) for *V. minor* reveals the interesting fact that the tunica of *V. rosea* consists of one less layer of cells than is found in *V. minor*. A similar variation in the structure of the tunica amongst different species of the same genus has been reported for *Viburnum* (Cross 1937b, 1938) and *Veronica* (Schmidt 1924).

GROWTH OF THE DIPLOID SHOOT APEX

An idea of the changes that occur in the apical meristem during the course of a plastochron, including the initiation of foliage leaves, may be obtained by studying figures 4–10 and 15–20. In figure 4 the narrow, columnar appearance of the cells in T–1 and T–2 provides evidence of recent mitotic activity. Although only anticlinal divisions occur in the tunica, the summit of the meristem is gradually elevated (increased in height) during the plastochron. It is apparent in figure 5 that this increase in height is a result of cellular activity in the corpus. All the cells of the first layer of the corpus except one cell near the center have divided periclinally (thus forming C–1 and C–2), and a slight growth of the derivatives has thrust the apex of the shoot upward somewhat. Below C–2 the cellular pattern is irregular in all figures. In figure 5 several groups of genetically related cells, each clearly derived from a single mother cell, and oriented in a manner suggestive of a rib meristem, may be seen in the central portion of the corpus. The mother cells of the rib meristem are derivatives of C–2, although formed perhaps during the preceding plastochron. In figure 6 a highly organized rib meristem may be seen, consisting of chains of cells which diverge from a region immediately below the central portion of C–2. The derivatives of the rib meristem augment the pith. Thus during the early stages of growth following foliar initiation the apical meristem may be regarded as consisting of four layers which cap the mother cells of a rib meristem. The relatively "shallow" nature of the apical meristem is apparent in figure 11, where the abrupt transition from densely cytoplasmic layers to highly vacuolate rib-meristem is striking. Except for relatively infrequent periclinal divisions (fig. 7), C–1 divides anticlinally during the plastochron, and as a result it appears as a discrete layer after the primordia of the next pair of leaves are initiated. However, the cells of C–2 divide extensively in various planes, and the derivatives form a massive core of tissue as the apex increases in size. Continued division and growth of the derivatives of C–2 elevate the surface of the meristem and generally thicken the meristem in vertical as well as lateral directions (figs. 7, 19).

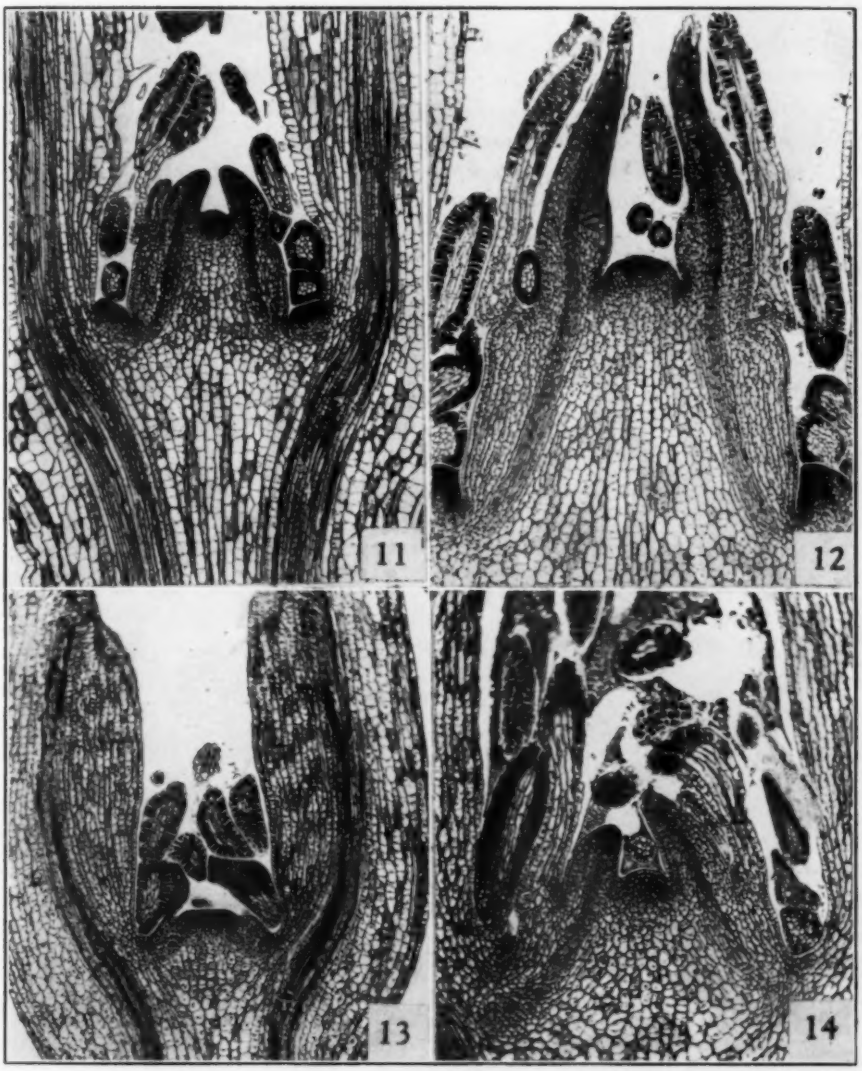
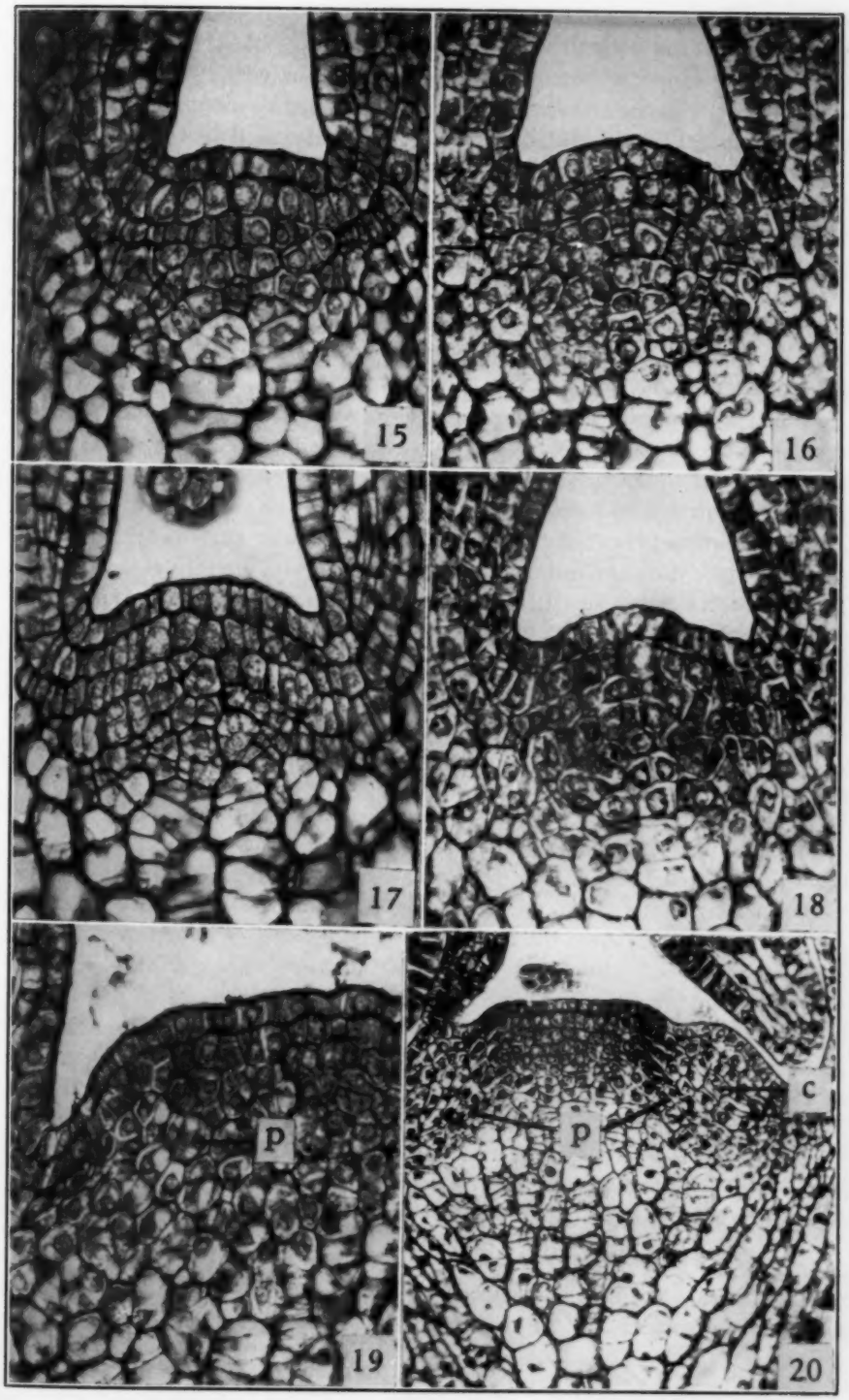


FIG. 11. Longisection of shoot apex showing apical meristem, young foliar primordia, young internode, axillary buds, glandular hairs. FIG. 12. Longisection of shoot apex cut perpendicular to plane of youngest foliar primordia. FIG. 13. Longisection of shoot apex in same stage of development as represented by fig. 12 but cut perpendicular to fig. 12. Note very young foliar primordia and lateral to them, young nodal and internodal regions. FIG. 14. Longisection of a colchicine-induced, tetraploid shoot apex of approximately the same stage of development as the one represented in fig. 11. × 70.

For a clearer understanding of the interrelated functions of the tunica and corpus in the growth of the shoot axis, it will be helpful to refer to figures 7 and 19, prepared from sections cut parallel with the longer transectional axis of the enlarging meristem shortly after leaf initiation (the youngest leaves are not in the plane of the paper). In these figures the layers of the tunica, except for the larger number of cells in each layer, are similar structurally to those seen in the previous figures, although the curvature of the apex is greater. Divisions in T–1 obviously had been entirely anticlinal up to the time that the material was fixed. Similarly in T–2 anticlinal divisions had prevailed at the summit, but in the margins or flanks of the meristem several cells in T–2 show evidence of having divided periclinally. Upon casual observation it might be supposed that such pericilinal divisions represent preliminary stages in the initiation of a new pair of foliar primordia. However, this is not the case; on the contrary, the periclinally divided cells of T–2 in figures 7 and 19 are related to the recently initiated, opposite foliar primordia, which are oriented in a plane perpendicular to that of the paper. In other words, these periclinal divisions are concerned with the development of the nodal and possibly the internodal portions of the shoot axis which are located immediately between and below the margins of the opposite leaf bases. From a study of many sections similar to those represented in figures 7 and 19 it appears that periclinally dividing cells in T–2 extend as a ring or ellipse throughout the entire circumference of the shoot apex during foliar initiation. In the plane of the long axis the derivatives contribute to the tissues of the young leaves; in the plane of the short axis they contribute to the cortex of the node and internode. This developmental feature was not described by Schmidt for *V. minor*. Figure 8 represents a later stage in the development of the nodal and internodal portions of the shoot axis which are associated with the youngest foliar primordia. The ridge-like appearance of such regions as seen in longitudinal sections is confusingly suggestive of foliar primordia, and only when a series of stages

Explanation of figures 15–20

FIG. 15. Longisection of shoot apex in early stage of plastochron cut parallel with plane of youngest leaves. Note three distinct layers at summit of meristem. FIG. 16. Longisection cut in same plane as fig. 15 but slightly later in plastochron, showing periclinal splitting of cells in first layer of corpus. FIG. 17. Longisection of apical meristem in still later stage of plastochron cut in same plane as figs. 15 and 16. Note transformation of derivatives of C–2 into rib meristem. FIG. 18. Similar to 16, showing large cells dominating first and second layers of tunica. FIG. 19. Longisection of apical meristem cut perpendicular to plane of youngest foliage leaves; periclinal splitting in flank of T–2 is associated with origin of node and associated internode of youngest leaves; *p*, provascular tissue. FIG. 20. Longisection apical meristem cut parallel with youngest foliar primordia, showing development of nodal and internodal region and vacuolation of cells in cortex; *p*, provascular tissue; *c*, cortex of young internode. Figs. 15–19, ×530; fig. 20, ×250.


15
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18
p
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c
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such as those represented by figures 7–10 and 20 is studied, does the real significance of the region become apparent.

To the left, in the youngest internode represented in figures 7 and 19, elongated cells indicating the origin of provascular tissue may be seen. Figures 8, 9, and 10, prepared from apices more advanced in the plastochron, confirm this interpretation. It is obvious that the provascular tissue of the axis is initiated from lateral derivatives of the corpus, which is in agreement with Schmidt's account of *V. minor;* however, in contrast to *V. minor* the provascular tissue in *V. rosea* is not differentiated immediately adjacent to derivatives of the tunica, but is separated from these by other derivatives of the corpus. Therefore, the corpus contributes to the cortex as well as to the stele of *V. rosea,* and accordingly is not to be regarded as equivalent to Hanstein's plerome.

When the length (long dimension as seen in transection) of the shoot apex is approximately 160 μ, new foliar primordia are differentiated in a plane perpendicular to the last pair, and they appear as small crescent-shaped protuberances located immediately centrad to the bulging nodal and internodal areas previously described. In figure 9, it may be seen that the earliest stages in foliar initiation are correlated with periclinal divisions in T–2. In later stages (fig. 10) the corpus extends as a core into the base of the primordium. The extent to which the corpus contributes to the tissues of the leaf was not determined precisely, but the results of studies by Johnson (1941) indicate that much of the foliar vascular tissue, at least that in the proximal regions, is derived from this growth zone. In *V. minor* derivatives of the corpus are not involved in foliar initiation, for in this species the foliar primordium is a product entirely of the tunica. The function of the third layer of the tunica of *V. minor,* i.e., the production of the vascular tissue of the leaf, is performed by the first layer of the corpus (however, the third layer of meristem) of *V. rosea.* The primordia grow vertically, perpendicular to the summit of the apical meristem. The elongated cells in the corpus (and youngest internode) near the base of the young foliar primordium in figure 9 represent the initiation of a provascular strand with which the leaf trace will be continuous. Similar provascular tissue may be seen in the second internode below, separated from that above by a single nodal cell marked X. As shown in figure 10 these two provascular strands become continuous; and at the upper limit of the strand a periclinally dividing cell, associated with the vertical differentiation of the provascular tissue into the leaf base, is evident. Thus the leaf trace of *V. rosea* apparently differentiates only in an acropetal direction, rather than both acropetally and basipetally, as described commonly for angiospermous genera.

THE SHOOT APEX OF TETRAPLOID PLANTS

In all basic structural features the apices of the tetraploid shoots are practically identical with those of the related diploid strain. A two-layered

tunica capping a central corpus is easily demonstrated (figs. 22, 24). The behavior of the tunica and corpus during the course of a plastochron, and the cellular contributions of these growth zones during the initiation of leaves, nodal and internodal portions, provascular tissue, pith, cortex, and epidermis are the same as described for the diploid variety; therefore, a second description will not be necessary.

However, it is apparent from a comparison of figures 11 and 14 that the tetraploid apices are considerably more massive than those of diploid shoots. Figures 21 and 22, prepared from diploid and tetraploid apices respectively, show that this is true not only of the apical meristem, but of the foliar primordia as well. The young tetraploid leaf in figure 22 is considerably thicker than the corresponding diploid leaf in figure 21, although both leaves are of approximately the same height, and both figures have the same magnification. Havas (1937), Eigsti (1938), Levan (1938), and others have reported that the increased size of a plant organ after treatment with colchicine is a result of increased cellular size rather than an increase in number of cells. It is apparent from only a casual comparison of tetraploid and diploid shoot apices (figs. 21–22, 23–24) that the increased size of the tetraploid meristem and foliar primordia is a result of increased cellular size rather than increased cellular number. It is further apparent that the *lateral* dimensions of the tetraploid cells have been increased more noticeably than the *vertical* dimensions. This is shown strikingly by figures 23 and 24, representing diploid and tetraploid meristem respectively, photographed with identical magnifications. In an effort to determine precisely what effect colchicine has upon the form and structure of the cells in the apical meristem of *Vinca*, a number of careful measurements were made of anticlinal walls, periclinal walls, and nuclei in the growth zones of both the diploid and tetraploid varieties. Shoot apices in various stages of growth following foliar initiation were selected for measuring. The measurements were taken only from T–1, T–2, and C–1 of each apex, because these regions are the primary centers of growth in the apical meristem. The average lengths of the periclinal and anticlinal walls in each layer were determined and the results for several apices are recorded in table 1.

It was found from measurements made of a series of diploid apices that the average dimensions of the cells in T–1, T–2, and C–1 do not vary greatly during the course of a plastochron (table 1). The greatest variation occurs in the anticlinal walls of C–1, as is shown by a comparison of apices 1, 2, and 3 in table 1. However, this is easily understood because the first layer of the corpus divides periclinally throughout its extent early in the course of a plastochron, and immediately after this division, before the derivatives have enlarged, the vertical dimensions of the cells in the new C–1 (upper layer

of derivatives) are considerably smaller than at other stages during the plastochron.

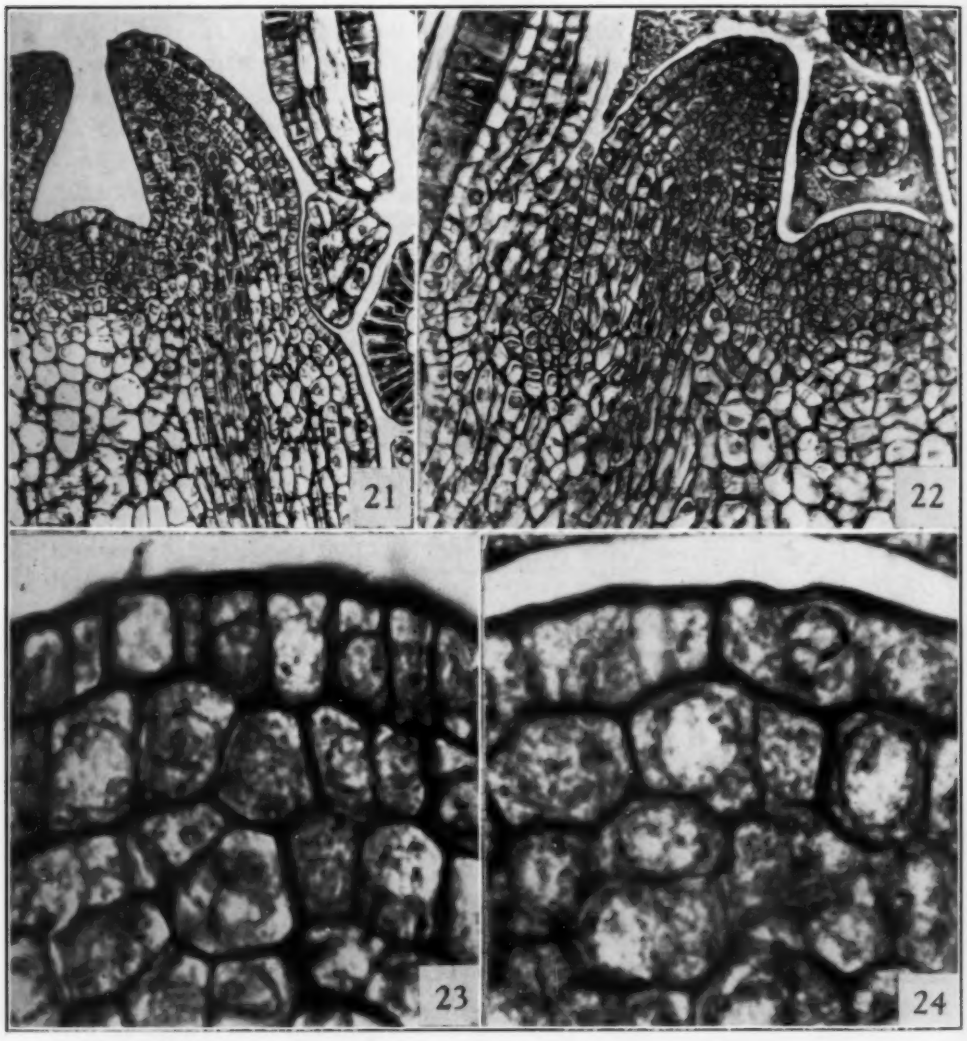

FIG. 21. Shoot apex and foliar primordium of diploid plant. FIG. 22. Shoot apex and foliar primordium of tetraploid plant. Note that the apical meristem is wider and not appreciably deeper than in the diploid. ×221. FIG. 23. Summit of apical meristem of diploid plant. FIG. 24. Summit of apical meristem of tetraploid plant. Note that the cells of the tetraploid have greatly increased lateral dimensions but that the vertical dimensions are approximately the same as those of the diploid. ×1105.

Measurements of the corresponding layers in tetraploid apices reveal the interesting fact that the anticlinal walls in T–1 and T–2 are certainly no

greater in *vertical* dimensions than are those of the diploid meristem. As a matter of fact, the average dimensions given in table 1 are somewhat less than those of the diploid. However, in C–1 the cells have slightly but definitely greater vertical dimensions in the tetraploid apices, as shown by measurements of the anticlinal walls. The *lateral* dimensions of the cells in all three layers are considerably greater in the tetraploid apices, as is shown by the average dimensions of the periclinal walls given in the table. From the figures here given it would appear that treatment with colchicine has increased the lateral dimensions of the cells in T–1 68.1 per cent, those in T–2 43.6 per cent, and those in C–1 58.9 per cent. This has resulted in considerably widened apices, but not noticeably deeper ones—because the vertical dimensions of the constituent cells have not been greatly altered.

The nuclei in the cells of both diploid and tetraploid apices occupy nearly all of the internal portions of the cells. Twenty-four nuclei from each strain were measured at random from T–1, T–2, and C–1. The diploid nuclei had an average size of 6.7 μ as compared with 8.9 μ for the tetraploid—representing a size increase of nearly 33.3 per cent following treatment with colchicine.

The tetraploid plants used in the present investigation have shorter and more massive stems, thicker and greener leaves, and somewhat larger flowers than their diploid ancestors. In the following paragraphs it is shown how all of these structural features seen in the mature plants, except those pertaining to the flower, are correlated directly with visible differences observed in the tunica and corpus.

The effect of colchicine upon the apical meristem of *V. rosea* is to increase the lateral dimensions of the cells to an extent varying roughly from one-half to two-thirds. This means that the entire apex is broadened in an amount equivalent to the sum of the increased dimensions of the constituent cells. A thicker pith and a generally more massive stem is the result. The vertical dimensions of the cells in the apical meristem are not increased however, and the mitotic rate of the tetraploid cells is apparently somewhat less than that of the diploid tissue. Both of these latter features are correlated with the fact that the tetraploid stems are thicker but not longer, and often are shorter, than the diploid.

The thicker, greener leaves of the tetraploid plants may be correlated similarly with the increased lateral dimensions of the apical meristem, when the method of their initiation is considered. The initial elevation of the foliar primordium occurs as a result of periclinal division in the cells of T–2, and therefore the elevation is in a direction perpendicular to the surface of the apical meristem. In the tetraploid apices the lateral dimensions of the cells of T–2 (T–1 and C–1 as well) have been increased markedly, and the derivatives of T–2 which constitute the internal portions of very young foliar

TABLE 1

Dimensions of cells in diploid and tetraploid meristems

Shoot apex number	Average dimensions of anticlinal and periclinal walls in T–1, T–2, and C–1								
	T–1			T–2			C–1		
	No. cells	Ant. walls	Per. walls	No. cells	Ant. walls	Per. walls	No. cells	Ant. walls	Per. walls
Diploid 1	12	9.1	4.5	11	9.5	5.5	11	8.3	5.5
Diploid 2	12	8.0	4.4	12	9.2	4.5	12	6.3	5.0
Diploid 3	14	8.3	5.0	15	8.9	5.1	13	8.0	5.5
Diploid 4	20	8.6	4.9	19	8.7	6.9	18	6.5	6.3
Diploid Average	14.5	8.5	4.7	14.3	9.0	5.5	13.5	7.3	5.6
Tetraploid 1	18	8.2	7.4	16	8.1	8.3	13	8.8	9.6
Tetraploid 2	12	7.9	7.1	11	9.0	7.5	12	7.4	7.3
Tetraploid 3	13	8.5	9.3	11	9.5	8.1	13	7.8	9.7
Tetraploid Average	14.3	8.2	7.9	12.7	8.9	7.9	12.7	8.0	8.9
Average percentage increase following treatment with colchicine		−3.5%	68.1%		−1.1%	43.6%		9.6%	58.9%

primordia accordingly have greater lateral dimensions than the corresponding cells in diploid foliar primordia of a comparable height. This results in tetraploid foliar primordia with considerably greater radial thickness, a feature which perhaps is correlated with the thicker and greener mature leaves. The possibility of a similar correlation of meristem characters with the somewhat larger tetraploid flowers will be investigated later.

DISCUSSION

The need for comprehensive information concerning the apical meristem in species of angiosperms is borne out by the fact that three (*Veronica*, *Viburnum*, and *Vinca*) of the relatively small number of investigated genera have species in which the structure of the shoot apex is not uniform with respect to the quantitative relationships of the tunica and corpus.

In *V. minor* three layers constitute the tunica—in *V. rosea* there are only two; however, as far as the fundamental features of growth in the two species are concerned, there are no great differences, for in each species derivatives of the outer three layers at the shoot apex form the foliar primordia and cortical tissues while the stele is a product of the more internally placed meristem. Thus the outer layer of the corpus makes essentially the same

cellular contributions in the shoot of *V. rosea* as are made by the third layer of the tunica in *V. minor*.

Schmidt (1924) has emphasized that the relative contributions of the tunica and corpus to leaf or bud initiation are dependent upon the quantitative relationships of these growth zones at the shoot apex. Schmidt's conclusion is supported by the results of the present investigation, for clearly the extent to which each of the growth zones contributes to the leaf and shoot axis in the genus *Vinca* is dependent upon their quantitative relationships in the apical meristem of each species, i.e., upon the number of layers in the tunica of each species. It would seem that the variations in quantitative relationships of the tunica and corpus that occur so commonly in the shoot apices of angiosperms may be of phylogenetic significance mainly with respect to problems of speciation. From a practical point of view they may prove to be of considerable significance in understanding problems associated with the origin of new varieties of plants, particularly the induction of new varieties by treatment with colchicine and other drugs.

In contrast to the procedure commonly described for seed plants, the leaf traces of *V. rosea* are differentiated acropetally into the foliar primordia and from the beginning are in continuity with provascular tissue previously formed in the two internodes and intervening internode immediately below. A similar acropetal differentiation has been described for the phyllode traces of *Acacia* (Boke 1940) and for the leaf traces of *Sequoia* (Crafts 1940). From an examination of a large number of genera of vascular plants, Wetmore[3] has concluded that strictly acropetal differentiation of leaf traces may be much more prevalent than has been suspected heretofore, and doubtless the subject should receive additional investigation. In this connection it is interesting to recall that Grégoire (1938) stressed the acropetal differentiation of provascular traces into floral parts, and used this feature in support of his idea that floral parts and foliage leaves are not homologous structures.

It is generally known that chromosomal number and cellular size may be increased by treatment with colchicine. The shoot apices of the induced tetraploid strain of *V. rosea* provide evidence that colchicine may also influence the *shape* or *form* of the cells in treated meristem and thereby affect the form of the adult plant. Similar formative effects were not reported for the apical meristem in tetraploid plants of *Datura* (Satina, Blakeslee, and Avery 1940), and it is clear that additional investigations are necessary before we can hope to understand the action and appreciate the possibilities of the drug in plant breeding.

SUMMARY

The shoot apex of *V. rosea* is described and compared with that of *V. minor* (Schmidt 1924).

[3] Private communication with Ralph H. Wetmore, Harvard University.

The shoot apex of *V. rosea* consists of a two-layered tunica and a central corpus, in contrast with that of *V. minor* for which a three-layered tunica has been described. With the exception of the outer layer of the tunica which produces the epidermis, the growth zones do not make precise contributions to the shoot axis, and therefore Hanstein's histogen-theory is not applicable to *V. rosea*.

Although the quantitative relationships of the tunica and corpus differ in the two species, the general features of growth at the shoot apices are similar, for in each species the outer three layers of the apical meristem make essentially the same contributions to the foliar primordia and shoot axis. Thus the functions of the tunica and corpus are correlated with their quantitative relationships.

The leaf traces differentiate acropetally into the bases of foliar primordia, rather than both acropetally and basipetally as is commonly reported for angiosperms.

The shoot apices of a colchicine-induced tetraploid strain of *V. rosea* are similar to those of the diploid parent in the quantitative relationships of the tunica and corpus. The apical meristem of the tetraploid plants is considerably wider than that of the related diploids, but the vertical dimensions are approximately the same. The increased width of the tetraploid apices is a result of increased lateral dimensions of the cells in the apical meristem. Cellular measurements indicate that treatment with colchicine as an average increases the lateral dimensions of the cells in T–1 about 68 per cent, those in T–2 43 per cent, and those in the first layer of the corpus 59 per cent. Significant differences in the vertical dimensions of cells of diploid and tetraploid meristems were not noted. The nuclei in tetraploid meristem are, as an average, approximately one-third larger than those of the diploid.

It is emphasized that colchicine affects the *shape*, as well as the size and chromosomal number, of the cells in the apical meristem of *V. rosea*. Visible changes in the meristem following treatment with colchicine are correlated with changes in the form of the adult plant.

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STUDIES ON AMERICAN HEPATICAE—III. VEGETATIVE REPRODUCTION IN BRYOPTERIS FRUTICULOSA

MARGARET FULFORD

(WITH THIRTEEN FIGURES)

Plants of *Bryopteris fruticulosa* Taylor collected at Punta Gorda, British Honduras, in November, 1932, exhibit an interesting example of vegetative reproduction by means of miniature shoots. These young shoots may be considered of two sorts depending on their place of origin on the plant, although they do not differ in their structure. The one sort originates from individual cells of the leaf and will be designated as leaf-cladia.[1] These are identical with the "Brutsprösschen" of Degenkolbe (2) and other authors. The other sort, the stem-cladia, originates on the stem and occupies the same position on the stem as the sexual branches. These belong to the category "Brutäste."

The leaf-cladia usually arise on the dorsal side of the ordinary, persistent leaves, especially after they are badly weathered or "eroded." They occur on any portion of the surface of the leaf and show no periodicity in their development, one leaf often bearing shoots of different sizes (see figure 1). They also occur on the male bracts.

This type of vegetative reproductive body on persistent leaves has been described in *Plagiochila* (1) and *Bazzania* (10). It is also frequent in many species with caducous leaves, associated with the caducous leaves. Evans (6) has described them in several tropical American genera, and more recently Degenkolbe (2) has given a comprehensive summary of "Brutsprösschen" in Hepaticae.

An ordinary leaf cell becomes more chlorophyllose than those adjacent and divides by means of a wall at right angles to the surface of the leaf (fig. 2), and one or both of the newly formed cells bulge on the dorsal surface (fig. 3). Then from one of these new cells one or two cells are cut off by transverse walls parallel to the leaf surface, so that a very short filament is formed. An apical cell with three cutting faces develops from the end cell after a few cells are cut off through anticlinal divisions. The new shoot is formed by the activities of this cell. The first cells cut off have bulging sides and can easily be distinguished even after the shoot has attained considerable length (figs. 4, 5). The first two leaves are very rudimentary, consisting of only three cells each. Each succeeding leaf becomes larger, and on the fifth or sixth leaf rudimentary lobules become evident. These, too, become

[1] Cladium (κλαδίον, diminutive of κλάδος, a branch or slip) is here proposed as a name for the small detachable branches which are effective in vegetative reproduction. The word was suggested by Dr. H. W. Rickett.

larger on succeeding leaves and are well developed on the ninth or tenth leaves. The typical (mature) leaves of these shootlets have more or less the same outline as the leaves of the parent plant, but they are, of course, very small, show no evidence of teeth on the margins, and have proportionately

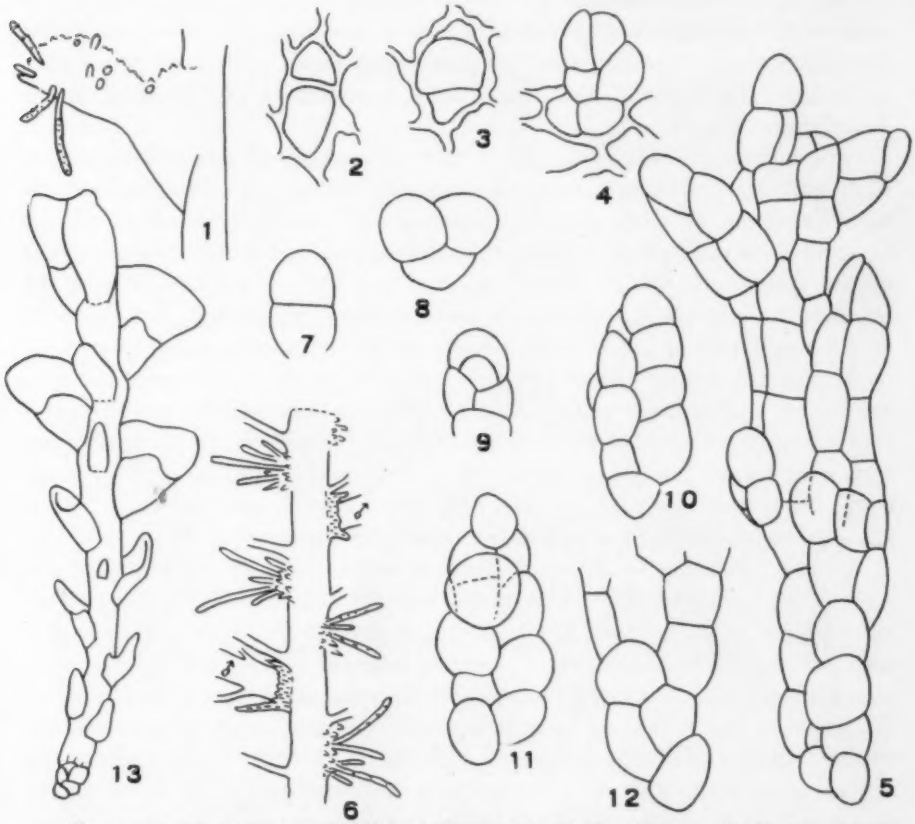

FIG. 1. Sketch of an "eroded" leaf showing brood shootlets on the dorsal surface. FIG. 2. A cell which has undergone the initial division in the formation of the propagule, ×375. FIGS. 3–4. Early stages in its development, ×375. FIG. 5. An older brood shoot showing the earliest leaves, ×375. FIG. 6. Diagram of a branch showing the position of the male branches and the tufts of brood branches just below the leaves. FIGS. 7–11. Stages in the development of the brood branch, ×375. FIG. 12. Basal portion of an older brood branch showing the rounded cells and the attachment cell, ×375. FIG. 13. A brood branch with well developed leaves and underleaves, ×90.

larger lobules. The first underleaf usually arises after the formation of the fifth leaf and is very rudimentary (see figure 5), triangular, and consists of three cells. Each successive one is larger and more completely developed. The mature underleaf is oblong and emarginate.

The stem-cladia are much more abundantly produced, often hundreds of

them occurring on a single stem. They are characteristically on the branches but are not uncommon on the main axis. They are produced in tufts of from ten to thirty or more just below a leaf, in the position of the sexual branches, often on the same axis with them (see figure 6).

The sexual branches are of the *Radula* type, that is, they "arise in a cortical cell adjacent to the base of a leaf on the basiscopic side and in the ventral portion of the segment" (8) and each has a well-developed sheath at its base. The tufts of stem-cladia arise in a similar position but do not develop such sheaths.

The individual branchlets of the tuft originate in disc-like areas of cortical cells just below the leaves. A transverse section of the stem shows a medulla fifteen or more cells in diameter, surrounded by a cortex of one layer of cells more or less rectangular in outline, not unlike the structure of the stem of *B. filicina* described by Evans (9). The inner cells of the medulla have relatively thin walls and are little pigmented, but the cells of the outer two or three rows, those nearest the cortex, have very thick walls and are deeply pigmented an orange-brown color. The cortical cells are larger, with thinner walls, and are a little less pigmented than the adjacent medullary cells. The cortical cells which give rise to the propagula are somewhat larger than those adjacent to them and do not have the typical deep, orange-brown color. In addition, the adjacent rows of cells of the medulla have thin walls and lack the usual pigmentation.

In the formation of the stem-cladia a cortical cell of the sort just described becomes packed with material and divides by means of a wall at right angles to the surface. The new cells bulge out and each one through a wall parallel to the periphery of the stem becomes two cells. The outer cell, by a series of divisions at right angles to the stem axis forms a mass of cells. Each one of the cells thus formed is capable of producing a new shootlet, through the formation of a few-celled filament, which in turn produces the apical cell of the new shoot, after the manner described for the development of the leaf-cladia from cells of the leaves (see figures 7–10). As in the latter, the early cells cut off are rounded in outline and irregularly arranged; the early leaves are rudimentary, consisting, for the most part, of only three or five cells; the well developed lobules appear on the ninth or tenth leaves; and the underleaves are at first very rudimentary, but successive ones become narrowly ovate, and finally oblong and emarginate (fig. 13). The branchlets often become more than 1.5 cm. in length while yet attached to the stem. The point of attachment is a single cell (see figures 5, 10–12) and the branchlets are easily separated by a slight movement. The break is schizolytic. Although there was no evidence in the material examined that these branchlets grow into normal plants, without doubt propagation by this method frequently occurs.

These stem-cladia are much less highly specialized than those described by Evans (3, 4, 5) for *Leptolejeunea, Drepanolejeunea* and *Odontolejeunea,* since they do not arise singly, possess sheaths, or develop the radicelliferous discs found in those genera. Degenkolbe (2) has discussed the development of "Brutäste" in his summary of the brood organs in hepatics. Similar slender filiform branches have also been noted in *B. tenuicaulis* Tayl. (7).

In addition to the above mentioned material from British Honduras in the Missouri Botanical Garden, plants with similar stem-cladia have been collected at Mirador, Mexico, by F. Müller; the east Coast of Guatemala, by Sereno Watson no. 58c; and in Bolivia by White (Mulford Exp. Amazon Basin no. 2133a) and are in the collections of the New York Botanical Garden.

The writer wishes to express her appreciation to Dr. A. W. Evans for his helpful criticism.

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NORTH AMERICAN RANUNCULI—III[1]

LYMAN BENSON

The first article in this series of five (Bull. Torrey Club **68**: 157–172. March, 1941) includes a key to the species of the section *Chrysanthe* of the subgenus *Euranunculus* and discussion of the first seven species. The other eleven species of the section are discussed in the second article (Bull. Torrey Club **68**: 477–490. October, 1941). This article deals with the sections *Echinella* and *Epirotes*. The delimitation of subgenera and sections was published in a paper entitled "The North American Subdivisions of *Ranunculus*" (Am. Jour. Bot. **27**: 799–807. 1940).

SECT. 2. ECHINELLA DC.

KEY TO THE SPECIES

Achenes with spines on the faces or margins.
- Mature achenes 5–7 mm. long, the spines straight; petals at least 4 mm. long.
  - Achenes with the margins produced into long spines; nectary scale not forming a pocket, broader than the adjacent part of the petal ..... 20. *R. arvensis.*
  - Achenes without spines on the margins, the faces spiny; nectary scale forming a pocket, much narrower than the adjacent part of the petal ..... 21. *R. muricatus.*
- Mature achenes 1–2 mm. long, the papillae on the faces produced into hooked spines; petals 1–2 mm. long ..... 22. *R. parviflorus.*

Achenes with no spines but the faces papillate, 1–2 mm. long.
- Petals 1–2 mm. long; papillae of the achenes produced into hooked hairs; sepals not reflexed ..... 23. *R. hebecarpus.*
- Petals 8–9 mm. long; papillae of the achenes not produced into hairs; sepals reflexed ..... 24. *R. sardous.*

20. RANUNCULUS ARVENSIS L. Sp. Pl. 555. 1753.

Waste ground and ballast; European weed; naturalized in North America; Yamhill and Marion Counties, Oregon; "Southern" Oregon; Potter Valley, Mendocino County and Mt. Bullion, Mariposa County, California; Grangeville, Idaho; Smithfield and Newton, Utah; metropolitan New York and New Jersey; Washington, D. C. Summer.

Type collection: "Habitat in Europae *australioris agris."*

21. RANUNCULUS MURICATUS L. S. Pl. 555. 1753. *R. echinatus* Vent. Jard. Cels. 73. 1800 (An. VIII of the French Revolution). *R. muricatus* var. *carolinianus* DC. Prodr. **1**: 42. 1824.

[1] References in the first article of this series to Abrams' Illustrated Flora of the Pacific States **2**: 1940 are erroneous, since that work did not appear at the time scheduled late in 1940. The two new combinations, *Ranunculus canus* Benth. var. *lactus* (Greene) L. Benson and *R. canus* var. *ludovicianus* (Greene) L. Benson, should be considered as published in the Bulletin of the Torrey Botanical Club **68**: 170 and 171. 1941, instead of in Abrams' Flora.

Meadows, stream and lake borders, and vernal rivulets at low elevations; Europe; naturalized in North America; Seattle, Washington; Newport, Port Orford and Myrtle Creek, Oregon; Del Norte, Lake, and Butte Counties to San Mateo, Contra Costa, and Stanislaus Counties, California; Arkansas; Coastal Plain from Texas to South Carolina. April and May.

Type collections: (1) *R. muricatus,* "*Habitat in* Europae *australis fossis & humentibus.*" (2) *R. echinatus,* "Environs de Charles-town." Charleston, South Carolina. (3) Var. *carolianus,* "Carolina and Virginia."

22. RANUNCULUS PARVIFLORUS L. Sp. Pl. ed. 2. **1**: 780. 1762. *R. trachyspermus* Ell. Sketch. **2**: 65. 1816. *R. parviflorus* var. *dimidiatus* Krause, Beih. Bot. Cent. **32** (2): 330. 1914.

Waste ground; Europe; naturalized in North America; Humboldt County, California; Eastern Arkansas and Houston, Texas, to Lexington, Kentucky, Virginia, northern Georgia and extreme northwestern Florida; Peekskill, New York; Bermuda and St. David Islands, Bermuda; at 1,100 meters elevation in Jamaica. Summer.

Type collections: (1) *R. parviflorus.* "*Habitat in* Europae *australis.*" (2) *R. trachyspermus,* "Collected in St. John's Berkley, by Dr. Macbride." Near Savannah, Georgia. (3) Var. *dimidiatus, Krause* "No. 5567. Bei Virginia Beach am 13 Mai." Virginia, 1890.

23. RANUNCULUS HEBECARPUS Hook. & Arn. *R. parviflorus* L. var. Torr. & Gray, Fl. N. Am. **1**: 25. 1838. *R. hebecarpus* Hook & Arn. Bot. Beech. Voy 316. 1840. *R. hebecarpus* var. *pusillus* Brew. & Wats. Bot. Calif. **1**: 9. 1876.

Shade of trees at 100–1,000 or 1,300 meters elevation; Latah County, Idaho; Wawawai, Washington; Columbia River Gorge; occasional in southwestern Oregon; Siskiyou and Modoc Counties and the whole foothill region of cismontane California, except the seaward North Coast Ranges; Santa Catalina Island; northern Baja California and Guadaloupe Island. Primarily oak woodland. March to May.

Type collections: (1) Unnamed variety, Torr. & Gray, "California, Douglas!" (2) *R. hebecarpus,* "California—Supplement. Where not otherwise mentioned, it is to be understood that the following species are from the collection of Mr. Douglas. They were presented by the Horticultural Society of London, in whose service Mr. Douglas was at the time he gathered them." (3) Var. *pusillus.* No type given. It and the typical species were reported from the "coast-ranges and foot-hills of the Sierra Nevada." No plants of *Ranunculus hebecarpus* warrant segregation as a variety.

24. RANUNCULUS SARDOUS Crantz, Stirp. Austr. Ed. 1. fasc. 2. 84. 1763. *R. parvulus* L. Mant. Pl. 79. 1767.

Waste places; Europe; naturalized mostly about seaports in North America; Columbia River at Portland, Oregon; Fortuna, Humboldt County, California; St. Louis; New York; Philadelphia; Norfolk and Meherrin River, Virginia; "Eastern" North Carolina; Savannah and Tybee Island, Georgia. May to July.

SECT. 3. EPIROTES (PRANTL) L. BENSON

KEY TO THE SPECIES

Roots not distinctly tuberous, if slightly fusiform-tuberous, the thickened portion not truncate, 0.5–2 or rarely 2.5 mm. in diameter; petals usually obovate or cuneate, rarely 2–3 times as long as broad.
Horizontal rootstocks not present.
Fruiting receptacle and head of achenes cylindrical or ovoid; achenes not stipitate or winged at the bases.
Stems 5 or more cm. long at fruiting time (measurement to the base of the highest pedicel).
Sepals not densely covered dorsally with reddish-brown hair.
Nectary scale ciliate (except rarely in *R. arizonicus*), the adjacent petal surface sometimes hairy also; achenes pubescent.
Stems scapose, rarely branching near the bases; nectary scale rectangular or nearly so; achene beak straight.
Each scape 4- or usually 8–12-flowered; dead leaf bases represented by numerous brown fibers; margin of the nectary scale free along the distal third; petals 2–3 times as long as broad, not emarginate; fruiting receptacle cylindrical, slender ..... 29. *R. arizonicus.*
Each scape 1–3- or 4-flowered; dead leaf bases not markedly fibrous; margins of the nectary scale adnate to the petal for almost their entire length; petals nearly as broad as long, sometimes emarginate; fruiting receptacle ovoid or ovoid-cylindrical, stout ... 30a. *R. cardiophyllus var.*
Stems not scapose, branching near the bases; nectary scale obdeltoid; achene beak recurved ..... 30. *R. cardiophyllus.*
Nectary scale and petal glabrous.
Margins of the nectary scale prolonged into 2 flaps attached most of their length to the blade of the petal, each flap 4–5 mm. long by 0.6 mm. broad; leaves dissected; plant practically glabrous. 31. *R. Eastwoodianus.*
Margins of the nectary scale not prolonged for more than 1 mm.
Fruiting receptacle 2–4 mm. long, 1–3 mm. in diameter; stems usually profusely branched and 8–25- or 60-flowered; achenes glabrous. (*R. arizonicus* is allied to this group of species as well as to *R. cardiophyllus.*)
Petals shorter than the sepals.
Achene beaks 0.1–0.3 or rarely 0.4 mm. long; petals two-thirds to five-sixths the length of the sepals; nectary scale laterally attached for its full length.
Herbage glabrous or nearly so; receptacle villous or rarely glabrous; leaves reniform, usually distinctly cordate; nectary scale notched (or truncate?) at the apex; head of

achenes ovoid; achene beak 0.1–0.2 mm. long; bracts of 3 or 5 narrow divisions, these broadest at the middles; roots filiform, rarely thickened ..... 25. *R. abortivus.*

Herbage villous; receptacle glabrous (rarely villous); leaves proximally truncate or almost attenuate; nectary scale truncate at the apex; head of achenes cylindrical or ovoid-cylindrical; achene beak 0.2–0.3 mm. long; bracts of 3–5 linear-oblanceolate divisions; some of the roots somewhat fusiform-thickened and some filiform on each plant. 26. *R. micranthus.*

Achene beaks 0.6–1 mm. long, curved or recurved; petals 1–1.5 mm. long, one-third to one-half the length of the sepals, broadly elliptic; nectary scale free laterally for half its length; bracts with 5 nearly linear lobes; roots all filiform; leaves reniform ..... 27. *R. allegheniensis.*

Petals longer than the sepals; achene beaks 0.4–0.6 mm. long, straight; petals 6–8 mm. long, twice the length of the sepals; nectary scale attached laterally through its whole length, truncate; bracts with 3 oblanceolate divisions; some of the roots fusiform and 1.5–2.5 mm. in diameter; leaves reniform, the lobes relatively few. 28. *R. Harveyi.*

Fruiting receptacle 4–16 (or rarely only 3) mm. long, usually 3–9 mm. in diameter; stems sparingly branched, each bearing 1–3 or sometimes 7–9 or rarely 11 flowers.

Sepals and usually the pedicels densely tomentose.

Petals twice as long as the sepals ..... 32. *R. pedatifidus.*

Petals scarcely longer than the sepals ..... 33. *R. Sabinii.*

Sepals and pedicels glabrous or thinly pilose.

Achenes obovate.

Radical leaf blades ovate to orbicular, not broader than long; achene beak 0.8–0.9 mm. long; stems 3–7- or rarely 11-flowered; achenes 50–100 in a head 7–17 mm. long. ..... 34. *R. inamoenus.*

Radical leaf blades reniform or semicircular, broader than long; achene beak about 0.3 mm. long; stems 1–3-flowered; achenes 20–45 in a head 4–6.5 mm. long ..... 35. *R. Allenii.*

Achenes almost oblong.

Petals, when fully expanded, 3–5 mm. long, the sepals the same length; achene beaks recurved, 0.5 mm. long; basal leaves proximally cordate ..... 36. *R. verecundus.*

Petals, when fully expanded, at least 60 per cent longer than the sepals, 8–18 (rarely 5) mm. long; achene beaks straight, 1 mm. long; leaves truncate or rounded at the bases.
The 3 primary divisions of the basal leaves once-lobed or entire; head of achenes cylindrical or ovoid-cylindrical ..... 37. *R. Eschscholtzii.*
The 3 primary divisions of the basal leaves again twice-divided into linear divisions; head of achenes ovoid. (See also the varieties *Suksdorfii* and *trisectus* of *R. Eschscholtzii*) ..... 38. *R. adoneus.*
Sepals densely covered dorsally with conspicuous *reddish-brown* hair.
Radical leaf blades reniform to cordate, semicircular, or nearly orbicular, palmately lobed or parted; petals obovate.
Receptacle glabrous; achene body about 1.5 mm. long ... 39. *R. nivalis.*
Receptacle brown-hispid; achene body occasionally 1.5, but ordinarily 1.8–2 mm. long ..... 40. *R. sulphureus.*
Radical leaf blades very narrowly elliptic, shallowly toothed at the apices; petals cuneate; receptacle glabrous. 41. *R. Macauleyi.*
Stems not more than 5 cm. long at fruiting time (measurement to the base of the highest pedicel).
Petals twice as long as the sepals, 5 mm. long by 4 mm. broad ... 42. *R. Grayi.*
Petals the same length as the sepals, 1.5–3.5 mm. long by 1–2.8 mm. broad ..... 43. *R. pygmaeus.*
Fruiting receptacle and head of achenes spherical or globose; achenes each with a broad thin stipe or winged base, except in *R. pygmaeus.*
Stems not more than 4 cm. long at fruiting time (measurement to the base of the highest pedicel) ..... 43. *R. pygmaeus.*
Stems 5 cm. long or longer.
Herbage pilose; petals obovate-spatulate, the nectary scales glabrous; achene beaks 0.3 mm. long ..... 44. *R. rhomboideus.*
Herbage glabrous; petals obovate, the nectary scales usually distally ciliate; achene beaks 0.6 mm. long ..... 45. *R. glaberrimus.*
Horizontal rootstocks produced about 4 cm. below the surface of the soil; flowering stems scapose; head of achenes hemispherical ..... 46. *R. verticellatus.*
Roots distinctly and conspicuously tuberous, the tubers truncate distally, 3–5 (rarely only 2) mm. in diameter; petals broadly oblanceolate ..... 47. *R. Jovis.*

25. RANUNCULUS ABORTIVUS L. Sp. Pl. 551. 1753. *R. nitidus* Walt. Fl. Carol. 159. 1788. *R. ruderalis* Greene, Am. Midl. Nat. **3**: 334. 1914. *R. Holmei* Greene, Am. Midl. Nat. **3**: 334. 1914. *R. michiganensis* Farwell, Rept. Mich. Acad. Sci. **17**: 169. 1916. *R. abortivus* var. *typicus* Fern. Rhodora **40**: 417. 1938. *R. abortivus* var. *acrolasius* Fern. Rhodora **40**: 418. *pl. 519. f. 1–2.* 1938.

Radical leaves simple or rarely some trifoliolate, reniform, 1–5 cm. long, 1–6 cm. broad, crenulate or crenate, some 3-lobed, -parted, or -divided, petioles 4–11 cm. long, stipular leaf bases scarious, 1–2 cm. long; cauline leaves

alternate, the bracts deeply once- or twice-parted to form 3 or 5 elliptic lobes, sessile; receptacle fusiform-cylindrical, about 2 mm. long in flower and 2–4 mm. long in fruit, sparsely villous.

Moist ground in rich woodland at low elevations; Juneau, Alaska, and British Columbia to Labrador, southern Colorado, eastern Texas and Chattachoochee, Florida. Northern coniferous, western pine, Northeastern pine and hardwood and Southeastern pine, and river bottom forests. March to June, depending upon locality.

Type collections: (1) *R. abortivus*, "*Habitat in* Virginia, Canada." (2) *R. nitidus*. Carolina. (3) *R. ruderalis*, "First observed by me as growing on a railway embankment near Linden station of the Baltimore & Ohio Railway, within the State of Maryland, but not far outside the District of Columbia, this in May, 1912." TYPE, *HGr. 13022–3*. (4) *R. Holmei*, "A common plant of low woodland borders and open thickets, in rich alluvial soil along the Potomac River & its tributaries in Maryland & Virginia." The following specimen is designated as a LECTOTYPE: Thicket near canal, below High Island, Maryland, *Greene*, Apr. 23, 1912, *HGr. 13027*. (5) *R. michiganensis*, "Swamp lands near Rochester, Michigan, Farwell, No. 3627, May 17, 1914." (6) Var. *acrolasius*, "Shelburne N. H., May 17, 1910, *Deane* (TYPE in Herb. N.E. Bot. Cl.). . . ." This is a northern and Rocky Mountain form with the younger portions of the plant (stems, cauline leaves, and pedicels) pubescent.

25 A. RANUNCULUS ABORTIVUS var. EUCYCLUS Fern. Rhodora **1**: 52. 1899. *R. abortivus* f. *giganteus* Gates, Trans. Kans. Acad. Sci. **33**: 28. 1930.

Stems elongated, slender and flexuous; radical leaf blades deeply cordate with a narrow basal sinus; 3.5–4.5 cm. long (on the axis), 4.5–6 cm. broad, the blade as a whole practically circular; cauline leaves like the typical species; fruiting receptacle slender.

Rich woods; Quebec to Newfoundland and south to New York and New England; Yates Center, Kansas, and Hope, Arkansas. Northern coniferous and Northeastern pine and hardwood forests. Early summer.

Specimens from Devil's Lake, North Dakota (*Lunell*, July 1, 1905, *NY.*) and from Vermont (*Carey*, *NY.*) have similar leaves but not the slender and flexuous stems.

Type collections: (1) Var. *eucyclus*, "First collected by Miss Kate Furbish at East Livermore, June, 1888." Maine. (2) F. *giganteus*, "The type specimen, 50 cm. high, collected June 5, 1928, three miles southeast of Yates Center, Kansas, deposited in the herbarium of the Kansas State Agricultural College, Manhattan, Kansas, by Mrs. C. E. Rogers" (O. E. Rogers on the label). The specimen was kindly loaned to the University of Arizona by Dr. F. C. Gates. The fruiting receptacle is of a nearly filiform type rarely equalled in narrowness in the typical species or the var. *eucyclus*, and the radical leaves are 4.5–6 cm. long (on the axis), or 8–9 cm. if the basal lobes are included. The basal sinus is about 3 cm. deep. The flowers are unknown. This form is truly remarkable for its size, but it is deficient in technical characters to differentiate it as a variety.

25 B. RANUNCULUS ABORTIVUS var. INDIVISUS Fern. Rhodora **40**: 418. *Pl. 518.* 1938.

Herbage a darker green than in the typical species; stems like the typical species; radical leaf blades shaped like those of the typical species, but the teeth very shallow; bracts cuneate, obovate, apically shallowly-lobed or -toothed.

Alluvial woods of bottom-land; Nottaway River Valley, Southhampton County, Southeastern Virginia. River Bottom Forest. April.

Type collection: "Three Creek, Drewryville, April 9, 1938, *Fernald & Long,* No. 7829 (TYPE in Gray Herb., ISOTYPE in Herb. Phil. Acad.). . . ."

26. RANUNCULUS MICRANTHUS Nutt. ex Torr. and Gray, Fl. N. Am. **1**: 18. 1838. *R. delitescens* Greene, Am. Midl. Nat. **3**: 333. 1914. *R. cymbalistes* Greene, Am. Midl. Nat. **3**: 333. 1914. *R. micranthus* var. *delitescens* Fern. Rhodora **41**: 543. 1939. *R. micranthus* var. *cymbalistes* Fern. Rhodora **41**: 543. 1939.

Low elevations; South Dakota to Arkansas and thence to southern Illinois, southern Indiana, and Kentucky; Massachusetts to the District of Columbia. April or May.

Type collections: (1) *R. micranthus,* " 'Margins of ponds throughout the upper & western part of Missouri, likewise in Arkansas, collected by *Dr. Pitcher.' Nuttall!*" The Pitcher specimen in the New York Botanical Garden is designated as a LECTOTYPE. It was collected at Ft. Gratiot (?). (2) *R. delitescens.* "Guttenberg, New Jersey, 12 May, 1895, by William Van Sickle. . . . Harper's Ferry, W. Va., 11 May, 1889, by F. V. Coville." (3) *R. cymbalistes,* "Known only as collected in extreme southern Indiana, 20 April, 1913, by Mr. Charles C. Deam, where it inhabits wooded knolls, under Pinus Virginiana & Quercus alba, the special locality 2 miles west of New Albany."

27. RANUNCULUS ALLEGHENIENSIS Britt. Bull. Torrey Club **22**: 224. 1895.

Moist woodland in New England (uncommon and not found in Maine) and in the mountains from Franklin County, Pennsylvania, to Waynesville, North Carolina. Northeastern pine and hardwood forests. May or early June.

Type collection: "Mountains of Virginia & North Carolina." The following specimen is designated as a LECTOTYPE, White Top Mountain, Grayson County, Virginia, *N. L. & E. G. Britton and A. M. Vail* in 1892, *NY.*

28. RANUNCULUS HARVEYI (A. Gray) Britt. Mem. Torrey Club **5**: 159. 1894. *R. abortivus* L. var. *Harveyi* A. Gray, Proc. Am. Acad. **21**: 372. 1886. *R. Harveyi* Greene, Erythea **2**: 189. Dec. 1, 1894. *R. Harveyi* var. *pilosus* Benke, Rhodora **30**: 200. 1928.

Moist woodland; Southern Missouri and Arkansas; vicinity of Tuscaloosa, Alabama (e.g., *Harper 3181, NY.*). Southern hardwood and river bottom forests. Late April and early May.

Type collections: (1) Var. *Harveyi,* "On damp rocks in Arkansas, *F. L. Harvey* and *Dr. Hass* [Hasse]." (2) Var. *pilosus,* "The type is from Rolla, Mo., Apr. 18, 1928, H. C. Benke 4575 in Field Museum."

29. RANUNCULUS ARIZONICUS Lemmon. A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. nudatus* Greene, Leafl. Bot. Obs. & Crit. **1**: 211. 1906.

Dry situations at 1,600–2,250 meters elevation; Greenlee and Santa Cruz Counties, Arizona, to Santa Rita, New Mexico. Western pine forest (?), southwestern coniferous woodland, and oak woodland. Flowering in the summer rainy season.

Type collections: (1) *R. arizonicus*, "Lemmon, in herb. Gray. . . . The plant sent by Mr. Lemmon with this name is the same as C. Wright's no. 837, also from Arizona, and which was taken for a form of *R. affinis* in the Botany of the Mexican Boundary." The Lemmon specimen is the type. It was collected in Rucker Valley, Chiricahua Mountains, Sept. 28, 1881, *Lemmon 585*. (2) *R. nudatus*, "Burro Mountains, at 7,500 feet, O. B. Metcalfe, 20 June, 1903." The TYPE is *HGr. 2815*.

30. RANUNCULUS CARDIOPHYLLUS Hook. Fl. Bor. Am. **1**: 14. *pl. 5. f. B.* 1829. *R. affinis* R. Br. var. *cardiophyllus* A. Gray, Proc. Acad. Phila. **15**: 56. 1864. *R. affinis* R. Br. var. *lasiocarpus* Torr. Bot. Wilkes Exped. **17**: 213. 1874. *R. affinis* var. *validus* A. Gray, Proc. Am. Acad. **21**: 371. 1886. *R. cardiophyllus* var. *pinetorum* Greene, Pittonia **4**: 144. 1900. *R. pedatifidus* J. E. Smith var. *pinetorum* Davis, Minn. Bot. Studies **2**: 483. 1900. *R. affinis lasiococcus* Torr. ex Piper, Contr. U. S. Nat. Herb. **11**: 273. 1906, as syn.

Stems erect, not rooting adventitiously, 2–4 dm. long and 2–4 mm. in diameter, 1–5-, or 8-flowered, fistulous, pilose, striate; radical leaf blades simple, cordate, 1–6 cm. long, 1–5 cm. broad, crenate, sometimes the apex lobed or rarely parted, proximally cordate and distally rounded, pilose, petioles 5–10 or 16 cm. long, pilose, stipular leaf bases 2–4 cm. long, not markedly fibrous after withering; cauline leaves alternate, the bracts divided into 3–7 linear lobes, sessile; petals 5, yellow, broadly cuneate-obovate, 8–15 mm. long, 6–13 mm. broad, the nectary scale ciliate on its apical margin with hairs nearly 1 mm. long (the surrounding petal surface often with similar hairs), forming a pocket, obdeltoid; achenes 50–125 in a cylindrical head 8–10 or usually 10–15 mm. long by 5–6 or usually 7–9 mm. in diameter, each achene obovate, 2 mm. long, 1.5 mm. dorsoventrally, 0.6–0.8 mm. laterally, smooth, finely canescent, margin inconspicuous, the achene beak slender, 0.6–1 mm. long, recurved; receptacle ovoid-cylindrical, 3–4 mm. long in flower, 7–14 mm. long in fruit, densely hairy.

Meadows in the mountains at 2,500–3,350 meters elevation southward and at 600–1,500 meters northward; Moose Mountain, Northwest Territory; Rocky Mountain system in Alberta and from Wyoming and the Black Hills to Northern Arizona and the northern edge of New Mexico. Western pine forest. Mostly July.

Type collections: (1) *R. cardiophyllus*, "Hab. from Canada to lat. 55°. In the central prairie & limestone districts. *Dr. Richardson. Drummond.* Alpine prairies in the Rocky Mountains. *Drummond.*" (2) Var. *lasiocarpus*, "Columbia River between the Spokane and Fort Colville." *Wilkes Expedition.* (3) Var. *validus*, "Taking the slender, high-northern form with even the leaves sometimes 'pedately multifid,' as the original of the species, the

above name may be given generally to the stouter and larger forms, of lower altitudes or elevations, with more succulent leaves, . . . to this belongs *R. cardiophyllus,* Hook., figured both in the Fl. Bor.-Am. & in Bot. Mag. t. 2999 but with the style too long." This name is considered to be a new one for *R. cardiophyllus* and to be based upon the same type. (4) Var. *pinetorum,* "'Abundant in pine woods, at Graham's Park, 7,800 ft.' southern Colorado, 12 May, 1899, C. F. Baker." The TYPE is *HGr. 2547.* (5) *R. affinis lasiococcus. Lasiococcus* apparently unintentionally substituted for *lasiocarpus.*

30 A. RANUNCULUS CARDIOPHYLLUS var. SUBSAGITTATUS (A. Gray) L. Benson, Am. Jour. Bot. **27**: 187. 1940. *R. arizonicus* Lemmon var. *subsagittatus* A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. subsagittatus* Greene, Pittonia **2**: 59. 1890.

Stems scapose, 1–1.5 or 2.5 mm. in diameter, usually unbranched below, 1–3- or 4-flowered, a little fistulous, glabrous or pilose; radical leaf blades simple, cordate or long-ovate or rarely subsagittate, 1.5–4.5 cm. long, 1–4 cm. broad, crenately toothed, proximally cordate (often deeply so) or rounded and distally rounded or obtuse or acute, petioles pilose or glabrous, stipular leaf bases 1–2 cm. long; cauline leaves all bracts, consisting of 1–5 linear divisions; petals 5, yellow, glossy on only the distal part, obovate or obovate-obdeltoid, sometimes deeply emarginate, 7–15 mm. long, 5.5–13 mm. broad, the nectary scale oblong; achenes mostly 20–50 in an ovoid head usually 5–6 mm. long by 4–6 mm. in diameter, the achene beak slender, straight; receptacle ovoid, 1–2 mm. long in flower and 4–7 mm. long in fruit.

Mountain meadows and stream banks at 2,300 to 3,000 meters elevation; east-central Arizona and west-central New Mexico. Mostly Western pine forest. July and August.

Type collection: "North Arizona in De La Vergne Park of the San Francisco Mountains, in wet ground, Lemmon." Aug., 1884.

30 B. RANUNCULUS CARDIOPHYLLUS Hook. var. COLORADENSIS L. Benson, Am. Jour. Bot. **27**: 804. *pl. 1. f. 7.* 1940.

Radical and lower cauline leaves ovate, the bases acute or obtuse, shallowly crenately-toothed; petioles of the radical leaves 8–18 cm. long; petals oblanceolate-obovate, 5–10 mm. long; otherwise like the typical species.

Mountain meadows at 2,800 meters elevation; Silverton, Colorado. Northern coniferous forest. July.

Type collection: "Silverton, Colorado, 9,500 elevation, *Herbarium of the State Agricultural College of Colorado* (collector not designated), July 3, 1898. Type in the New York Botanical Garden." An isotype from the Colorado State College Herbarium has been examined.

31. RANUNCULUS EASTWOODIANUS L. Benson, Am. Jour. Bot. **27**: 804. *pl. 1. f. 13.* 1940.

Known only from the type collection at Skagway, Alaska. Northwestern coniferous forest.

Closely allied to *R. pedatifidus* J. E. Smith. The species is named for Miss Alice Eastwood, Curator of the Herbarium of the California Academy of Sciences.

Type collection: "Skagway, Alaska, *Louise Huffine*, summer 1925, *California Academy of Sciences 138,383.*"

32. RANUNCULUS PEDATIFIDUS J. E. Smith in Rees. Cyclop. **29**: *R.* sp. No. 72. 1819. *R. affinis* R. Br. Bot. App. Parry's 1st Voy. 265. 1824. *R. affinis* var. *leicocarpa* Trautv. Middendorf's Reise **1**: 62. 1847. *R. vicinalis* Greene, Pittonia **4**: 145. 1900. *R. apetalus* Farr, Ottawa Nat. **20**: 110. 1906. *R. pedatifidus* var. *leicocarpus* Fern. Rhodora **19**: 138. 1917.

Meadows in the Rocky Mountains at 2,800–3,500 meters in Colorado and at 800–1,500 meters in Alberta and tundra at low elevations on the arctic plains; Northern Asia; Yukon to Baffin Island, Labrador, and Greenland and southward to Alberta and Saskatchewan; Wyoming (Albany County) and Colorado. Arctic-Alpine grassland and northern coniferous forest. June and July.

An apetalous form occurs in the Rocky Mountains from the Athabasca River to Banff and in Gilpin County, Colorado. It was collected also by Hall and Harbour in Colorado in 1862 (*U.S.*).

Type collections: (1) *R. pedatifidus*, "Native of Siberia. Four specimens from that country are in the Linnaean herbarium. . . ." (2) *R. affinis*, "Collected in Melville Island, By the officers of the Expedition." "Chiefly in the vicinity of Winter Harbour . . . herbaria of Captain Sabine, Mr. Edwards, Mr. James Ross, Captain Parry, Mr. Fisher, & Mr. Beverly." (3) Var. *leiocarpa*, "In speciminibus taimyrensibus omnibus Ranunculi affinis R. Br. ovaria prorsus glabra sunt. . . ." Fernald's application of this varietal epithet was to a glabrous-fruited population best-developed in eastern Arctic America. Cf. also Fernald, Rhodora **36**: 93–96, 97. pl. 279–80. 1934. (4) *R. vicinalis*, "At Fort Selkirk on the Yukon River, in dry gravelly soil, 9 June, 1899, M. W. Gorman." (5) *R. apetalus*, "By the roadsides at Banff, Alberta."

A form collected on Mt. San Francisco, Arizona (*Little 4632, Sac*), and on loose calcareous slopes near snow banks at 11,800 feet on the northeast side of Delano Peak in the Tushar Range in Piute County, Utah (*Maguire 19278*, Herbarium of Utah State College) may be a new variety. It has the following characters: stems 4–15 cm. long; radical leaf blades 1–2 cm. long, deeply lobed or cleft into simple lobes, the upper lobes erect, the lower markedly divergent or somewhat reflexed; petals none.

33. RANUNCULUS SABINII R. Br. App. Parry's 1st. Voy. 264. 1824.

Wet ground in arctic regions; Melville Island to Ellesmere Land and northwestern Greenland. Arctic-alpine grassland. July and August.

Type collection: "Collected in Melville Island, By the Officers of the Expedition." "Chiefly in the vicinity of Winter Harbour. . . ." "Planta inter R. nivalem et Pygmaeum media in Herb. *D. Sabine* extat."

34. RANUNCULUS INAMOENUS Greene, Pittonia **3**: 91. 1896. *R. affinis* R. Br. var. *micropetalus* Greene, Pittonia **2**: 110. 1890. *R. micropetalus* Rydb. Bull. Torrey Club **29**: 158. 1902.

Hirsute to subglabrous terrestrial perennials; radical leaf blades simple and ovate, obovate, or orbicular, 1–4 cm. long, 1–3.5 cm. broad, at least some

radical leaves on each plant crenate, rarely some 3-lobed or -divided, proximally more or less attenuate and distally rounded, glabrous or appressed-pubescent, petioles 4–10 cm. long, appressed-pubescent, stipular leaf bases 1.5–2.5 or rarely 4 cm. long; cauline leaves alternate, the bracts of 3–5 nearly linear lobes, sessile; pedicels 3–10 mm. long in flower and 10–50 or rarely 70 mm. long in fruit, appressed-pubescent; sepals narrowly obovate, 3–5 mm. long, about 2–2.5 mm. broad; petals narrowly elliptic to obovate, 2.5–8 mm. long, 2–4 mm. broad; achenes 60–100 in a cylindric or barrel-shaped head 7–17 mm. long by 6–8 mm. in diameter, each achene nearly obovate, about 1.5 mm. long, 1.3 mm. dorsoventrally, 0.5–0.6 mm. broad laterally, smooth, densely short-pubescent, margin inconspicuous, the achene beak slender, 0.8–0.9 mm. long, recurved; receptacle slender and cylindric, 2–3 mm. long in flower and 6–15 mm. long in fruit, hispid.

Moist ground in the mountains at 2,000 to 3,000 meters elevation; Rocky Mountain System from Alberta to Mt. San Francisco, Arizona and the Sacramento Mountains, New Mexico; in Idaho collected in only Custer County. Western pine (lodgepole pine) forest. Mostly June and July.

Type collections: (1) Var. *micropetalus*, "*R. Arizonicus*, var. *subaffinis* Greene," Pittonia **2**: 60. 1890, "not of Gray," Proc. Am. Acad. **21**: 370. 1886. "On the San Francisco Mountain (which some recent explorers and visitors effect to call Mt. Agassiz) it grows along cold subalpine brooklets where it is associated with *Mertensia Siberica*, *Primula Parryi*, etc." Greene's collection from Mt. San Francisco in 1889 is designated as a LECTOTYPE. It is *HGr 1198*. The petals of the type specimen are 4–5 mm. long. The short-petalled and small-fruited form, which includes practically every specimen from Utah, Arizona, and New Mexico, most of those from the northern Rocky Mountains, and many from Colorado might be recognized as a variety based upon *R. affinis* var. *micropetalus*. However, gradual intergradation is found in both characters, and it seems better to consider *R. inamoenus* as variable in size of flowers and fruit, even though small petals and small fruit commonly accompany one another, and the two characters are found together through a large but indefinite geographical range. (2) *R. inamoenus*, "Common in the whole Rocky Mountain Region, at middle elevations, and hitherto erroneously treated as a variety of the arctic *R. affinis.*" That in 1890 Greene considered the central and northern Rocky Mountain plant somewhat different from his variety *micropetalus* on Mt. San Francisco, Arizona, is shown by the following statement, Pittonia **2**: 110. 1890, "It [var. *micropetalus*] differs from the Colorado and northern *R. affinis* only in its much more slender habit, minute flowers, and long cylindrical head of achenes." Since there is no recorded change of opinion between 1890 and 1896, it may be assumed that the variety *micropetalus* is not the "variety of the arctic *R. affinis*" mentioned by Greene in 1896 and that the species *inamoenus* was based upon a different type. This viewpoin was taken by Rydberg, Fl. Colo. 145. 1906. Coulter, Man. Rocky Mt. Bot. 8 1885, recognized two varieties of *R. affinis* for the Rocky Mountains. One was based upon *R. cardiophyllus* Hook. (*R. affinis* var. *cardiophyllus* A. Gray, Proc. Acad. Phila. **15**: 56. 1864, which has now a later typonym, *R. affinis* var. *validus* A. Gray, Proc. Am. Acad. **21**: 371. 1886.) Since the variety *cardiophyllus* of Coulter's Manual is described as having "*flowers an*

inch in diameter," it could not have been the type of *R. inamoenus* with the whole "corolla 3–5 lines broad." The other variety was identified by Coulter as *R. affinis* var. *leiocarpus* Trautv. and described as having small flowers, and it is probable that Greene had this variety in mind when he described *R. inamoenus*, although the proof is not necessarily adequate. Since Greene gave no type and only a vague reference to a variety of *R. affinis*, it is necessary to establish the identity of the species *inamoenus* by reference to the Herbarium Greeneanum, which contains 15 or 20 specimens. The following were collected by Dr. Greene prior to publication of the species, Nov. 9, 1896: Upper Bear Creek, Colorado, *Greene* in 1889; Dale Creek, Wyoming, *Greene* June 30, 1896. The writer designates the Dale Creek specimen, *H. Gr. 2639* and *2648*, as a LECTOTYPE.

Significant specimens: IDAHO: Bonanza, Custer County, *Macbride & Payson 3471, NY;* Cape Horn, Custer County, *Macbride & Payson 3621, NY.* COLORADO: (all with fruit larger than usual, 2 mm. long): Eldora to Baltimore, Gilpin County, *Tweedy 5688, NY;* Berthoud Pass, 11,000 feet, *Tweedy 5689, NY* (achene beaks nearly straight); Cuchara River above La Veta, 2,100 meters, *Rydberg & Vreeland 6244, NY.*

34 A. RANUNCULUS INAMOENUS var. **alpeophilus** (A. Nels.) L. Benson, comb. nov. *R. alpeophilus* A. Nels. Bull. Torrey Club **26**: 350. 1899. *R. utahensis* Rydb. Bull. Torrey Club **29**: 158. 1902. *R. inamoenus* var. *alpeophilus* L. Benson in Abrams, Ill. Fl. Pac. Sts. **2**: (perhaps appearing in advance of this paper).

Herbage practically glabrous; radical leaf blades 3-parted or some of them 3-lobed; achenes and usually the receptacle glabrous; otherwise like the typical species.

Moist slopes in the mountains at mostly 2,500 to 3,000 meters elevation; Yoho Valley, British Columbia; Wyoming and the East Humboldt (Ruby) Mountains, Nevada to Utah and Central Colorado. Western pine forest (mostly lodge pole pine). Summer.

Type collections: (1) "Several collections of it have been secured, from nearly alpine stations in the State of Wyoming, growing in moist, rich soil. Nos. 1780 and 4211 by the writer, and no. 5252 by Mr. Elias Nelson may be cited as typical." The TYPE is established by the following excerpt from a letter received from Dr. Aven Nelson and dated December 21, 1938: "Replying to your valued inquiry concerning *Ranunculus alpeophilus*, I will state that my number which I have designated as type and which I find in our type case is 4211, Battle Creek Mountain, August 17, 1897, collected by myself." (2) *R. utahensis*, "UTAH: Alta, Wasatch Mts., 1879, *M. E. Jones, 1130.* (Type in herb. Columbia University.)" This is a form with thick leaves and robust stems.

34 B. RANUNCULUS INAMOENUS var. SUBAFFINIS (A. Gray) L. Benson, Am. Jour. Bot. **27**: 187. 1940. *R. arizonicus* Lemmon var. *subaffinis* A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. subsagittatus* (A. Gray) Greene var. *subaffinis* Greene, Pittonia **2**: 110. 1890. *R. subaffinis* Rydb. Bull. Torrey Club **24**: 246. 1897.

Stipular leaf bases 2.5–3 cm. long; pedicels 10–33 mm. long in flower and 60–80 mm. long in fruit; sepals obovate, 5–7 mm. long, 3.5–4.5 mm. broad;

petals mostly obovate or obovate-lanceolate, 6–9 mm. long, 2.5–7 mm. broad; achenes about 50–60 in an ovoid or cylindric head 6–11 mm. long by 5–7 mm. in diameter, each achene about 2–2.3 mm. long, 1.5–1.7 mm. dorsoventrally, the beak about 1.5–2 mm. long, straight (or bent or curved out of position in herbarium specimens), the margin a little more conspicuous than in the typical species or some achenes showing evidence of a very broad margin.

Moist ground near timber line at about 3,400 meters elevation; Mt. San Francisco, Arizona. Northern coniferous forest. June and July.

Type collection: "Mt. Agassiz [Mt. San Francisco], *Lemmon." 4152,* collected near the summit at 12,000 feet elevation, September, 1884.

Significant specimens. ARIZONA: Mt. San Francisco, *Greene,* in 1889, *HGr, NY, Mearns* in 1887, *NY;* San Francisco Peaks, margin of the crater, 10,300 feet, *L. Benson 9628, B, UA;* San Francisco Peaks, *Whiting & Sanders* in 1935, *UA;* Near Flagstaff, *P. L.* in 1928, *UA,* Mt. San Francisco, *Little 4697, Sac.*

35. RANUNCULUS ALLENII Rob. Rhodora **7**: 220. 1905.

Meadows at 950–1300 meters (or lower northward); Akpatok Island and the Labrador Peninsula Labrador to Gaspe County, Quebec. Arctic-alpine grassland and northern coniferous forest. July and August.

Type collection: "GASPE COUNTY, QUEBEC: on flood plain of an alpine Brook, north face of Mt. Albert, alt. 770 to 1100 m., 14 August, 1905. *J. F. Collins & M. L. Fernald,* no. 83. (Type, in herb. Gray.)"

36. RANUNCULUS VERECUNDUS Rob. *R. verecundus* Rob. apud Piper, Contr. U. S. Nat. Herb. **11**: 274. 1906. *R. ramulosus* Jones, Contr. W. Bot. **14**: 47. 1912.

Wet slopes near timber line from near sea level (northward) to 3,000 meters elevation (southward); rare but widely distributed; Russell Fiord, Central Alaska; Sawback Mountain, Alberta; Mt. Stuart and Mt. Adams, Washington; Strawberry Mountains, Oregon; Woolly Creek, Siskiyou County, California (?); Custer and Blaine Counties, Idaho; Long Baldy, Little Belt Mountains and Glacier National Park, Montana. Arctic-alpine grassland. July and August.

Type collections: (1) *R. verecundus,* "Wet, gravelly places, Mt. Paddo [Adams], alt. 1850–2150 meters, July 31, 1883, *W. N. Suksdorf 93.* (Type in Hb. Gray.)" (2) *R. ramulosus,* "Swift Current Pass, Glacier National Park, 7,000 feet, *M. E. Jones* August 11, 1910." Herbarium of Pomona College.

Significant specimens. ALASKA, WASHINGTON, OREGON, CALIFORNIA, and IDAHO, cf. L. Benson, Am. Jour. Bot. **23**: 170. 1936. ALBERTA: Sawback Mountain, *Sanson 140, NY.* MONTANA: Long Baldy, Little Belt Mountains, *Flodman 469, NY;* Mineral Park, Glacier National Park, 7,000 feet, *Jones* in 1910, *P;* Swift Current Pass, Glacier National Park, 7,000 feet, *Jones* in 1910, *P;* Sexton Glacier, *Standley 17230, US.*

37. RANUNCULUS ESCHSCHOLTZII Schlect. Animad. Ranunc. **2**: 16. *pl. 1.* 1820. *R. nivalis* L. var. *Eschscholtzii* S. Wats. King's Rept. **5**: 8. 1871.

R. ocreatus Greene, Pittonia **4**: 15. 1899. *R. Helleri* Rydb. Bull. Torrey Club **29**: 158. 1902. *R. Eschscholtzii* var. *Helleri* L. Benson, Am. Jour. Bot. **23**: 169. 1936.

Caudex 1–2 cm. long, 3–6 mm. in diameter; radical leaf blades simple, semi-circular to reniform, 1.3–3 cm. long, 2.5–4 cm. broad, deeply 3-parted, the middle lobe again 3-lobed or entire, the lateral asymmetrically 3–7-parted, the ultimate lobes and sinuses rounded, the blade proximally truncate or rounded, petioles 3–8 cm. long, stipular leaf bases 1–1.5 cm. long, annually deciduous or disintegrating; petals 5 or usually 7–10 mm. long, 5–10 mm. broad; achenes glabrous.

Boreal and Alpine meadows and talus slopes from the Aleutian Islands and coastal Alaska to Crater Lake and scattering stations in the central Sierra Nevada, California, to the Wallowa Mountains in Eastern Oregon, to the East Humboldt or Ruby Mountains in Nevada, and to Alberta, Utah, and Colorado; Mt. San Francisco, Arizona; possibly New Mexico. Arctic-Alpine grassland. July and August.

The form south of the Canadian boundary has commonly an entire and lingulate middle leaf lobe (previously described as var. *Helleri*). A Utah and Colorado form has the stipular leaf bases often 1.5–2.5 cm. long (*R. ocreatus* Greene).

Type collections: (1) *R. Eschscholtzii*, "Hab. in insulis Unalascha et St. Georgii (de Chamisso)." (2) *R. ocreatus*, "Collected by Baker, Earle, & Tracy on Mt. Hesperus, Colorado, 2 July, 1898 (n. 912)." The TYPE is *HGr. 2740*. (3) *R. Helleri*, "IDAHO: near Lake Pend d'Oreille, 1892, *Sandberg, MacDougal, & Heller 842* (type in N. Y. Bot. Gard.)." The type has not been located at the New York Botanical Garden, but an ISOTYPE is in the Dudley Herbarium at Stanford University.

Significant specimens of *R. Eschscholtzii* and its Pacific States varieties, cf. L. Benson, Am. Jour. Bot. **23**: 169–170. 1936; also CALIFORNIA: Piute Mt., Sierra Nevada, *Jepson 4579 J;* Mt. Dana, Yosemite National Park, *M. S. Baker 4293 b* (Santa Rosa Junior College Herb.) and a few other collections from the central Sierra Nevada.

KEY TO THE VARIETIES

Ultimate basal leaf lobes and sinuses usually sharply acute, rarely obtuse in var. *eximius*.
- Basal leaf blade deeply parted, the middle lobe again 3-lobed ..... 37A. var. *Suksdorfii*.
- Basal leaf blade cleft, rarely parted, the middle lobe entire ..... 37B. var. *eximius*.

Ultimate basal leaf lobes rounded or obtuse, at least not sharply acute.
- Caudex 1–2 cm. long, unbranched; scarious or thickened stipular leaf bases 1–2 cm. long, deciduous or disintegrating annually; achenes glabrous ..... 37. *R. Eschscholtzii*.
- Caudex 1.5 or 3–7 cm. long, often branched; thickened stipular leaf bases 1.5–3 cm. long, usually persistent for 2 or more seasons.
  - Middle basal leaf lobe again 3- to 7-lobed; achenes pubescent or glabrous; leaves deeply parted ..... 37C. var. *trisectus*.
  - Middle basal leaf lobe entire, or very rarely 3 lobed; achenes glabrous; leaves usually cleft, rarely parted ..... 37D. var. *oxynotus*.

37 A. RANUNCULUS ESCHSCHOLTZII var. SUKSDORFII (A. Gray) L. Benson, Am. Jour. Bot. **23**: 170. 1936. *R. Suksdorfii* A. Gray, Proc. Am. Acad. **21**: 371. 1886.

Caudex 1–1.5 or rarely 2.5 cm. long, 3–5 or 7 mm. in diameter; radical leaf blades thin, deeply 3-parted, the middle lobe again 3-lobed, the ultimate lobes and sinuses sharply acute, scarious stipular leaf bases 1–2 cm. long, annually deciduous or disintegrating; petals 7–11 mm. long, 5–10 mm. broad; achenes glabrous.

Mountain meadows and slopes at 1,700–2,000 meters elevation; Washington in the Olympic and Cascade Mountains; Idaho; Western Montana; Northwestern Wyoming. Arctic-Alpine grassland. July and August.

Plants from Idaho, especially the southern part, and from Wyoming are intermediates between var. *Suksdorfii* and *Ranunculus adoneus* A. Gray var. *alpinus* (S. Wats.) L. Benson.

Type collection: "Mt. Adams, Washington Terr., at 6,000 to 7,000 feet, in damp ground, *Suksdorf*," 1884.

37 B. RANUNCULUS ESCHSCHOLTZII var. **eximius** (Greene) L. Benson, comb. nov. *R. eximius* Greene, *Erythea* **3**: 19. 1895. *R. saxicola* Rydb. Mem. N. Y. Bot. Gard. **1**: 64. 1900.

Caudex 1–2 cm. long, 3–7 mm. in diameter; basal leaves usually thin, cleft or rarely parted, the middle lobe entire, the ultimate lobes and sinuses sharply acute, or rarely somewhat obtuse, scarious stipular leaf bases 1–2 or 2.5 cm. long, annually deciduous or disintegrating; petals 8–12 or sometimes 17 mm. long, 6–11 or 19 mm. broad; achenes glabrous or rarely hairy.

Alpine meadows at 2,300–3,000 meters; mountains of Western Montana and Northwestern Wyoming; Big Horn Mountains and Battle, Carbon County, Wyoming (*Tweedy* in 1901); Fremont County, Idaho; La Sal Mountains, Southeastern Utah; Mt. San Francisco, Arizona. Arctic-Alpine grassland. July and early August.

This variety is related to *R. adoneus*.

Type collections: (1) *R. eximius*, "A most beautiful alpine and subalpine species of the Rocky Mountains in Colorado, Wyoming, and Idaho, apparently somewhat rare, but gathered sparingly, and in poor specimens even by Hall and Harbour, in whose collection it is mixed with *R. adoneus* as far as distributed. Better specimens have been obtained by Mr. Buffum of Laramie." The following specimen is designated as a LECTOTYPE: Little Bald Mountains, *B. C. Buffum* in 1892, *HGr 2592*. (2) *R. saxicola*, "MONTANA: Cedar Mountain, July 16, 1897, *Rydberg & Bessey, 4112* and *4113;* Mill Creek, 1887, *Tweedy 192*. YELLOWSTONE PARK: Electric Peak, August 18, 1897, *Rydberg & Bessey 4111;* 1895, *Tweedy, 192;* Mt. Holmes, 1884, *Tweedy, 301.*" *No. 4112* of *Rydberg & Bessey* from Cedar Mountain, Montana is designated as a LECTOTYPE. It is in the New York Botanical Garden.

Significant specimen. ARIZONA: Mt. San Francisco, 10,500 ft., *Whiting & Sanders* Cat. No. 756/1060, Museum of Northern Arizona Herbarium.

37 C. RANUNCULUS ESCHSCHOLTZII var. TRISECTUS (Eastw.) L. Benson, Am. Jour. Bot. **23**: 170. 1936. *R. trisectus* Eastw. apud Rob. Proc. Am. Acad. **45**: 394. 1910.

Caudex 1 or 3–6 cm. long, 4–7 mm. in diameter, usually branched; basal leaves usually thin, deeply 3-parted, the middle lobe again 3- to 7-lobed, scarious stipular leaf bases 1.5–2.5 cm. long, usually persistent for a season or more after death of the leaf; achenes hispid or glabrous.

Mountain slopes and meadows at 2,000–3,000 meters elevation; Yoho River, British Columbia and Spray River, Alberta; Wallowa, Strawberry, and Steen Mountains, Eastern Oregon; Payette Lake, Idaho; Black Rock Creek, Teton National Forest, Wyoming. Arctic-Alpine grassland. Mostly July.

Closely related to *Ranunculus adoneus*.

Type collection: "Alpine Wallowa Mountains, Eastern Oregon, Altitude 2745 m., growing at the base of cliffs, *William C. Cusick* No. 3200."

37 D. RANUNCULUS ESCHSCHOLTZII var. OXYNOTUS (A. Gray) Jepson, Fl. Calif. 1: 537. 1922. *R. oxynotus* A. Gray, Proc. Am. Acad. **10**: 68. 1875.

Caudex 3–7 mm. long, 5–12 mm. in diameter, often branched; basal leaves thick, cleft or rarely parted, the middle lobe entire and lingulate or rarely (Tulare County) 3-lobed, the 2 lateral lobes crenate, stipular leaf bases thick and persistent for one or more seasons; achenes glabrous.

Mountain meadows and talus slopes at 3,000–3,850 meters; California in the Warner Mountains, in the Sierra Nevada from Mt. Stanford (Castle Peak), Sierra County to Tulare County, in the White Mountains of Inyo County, and in the San Bernardino and San Jacinto Mountains. Arctic-Alpine grassland. Mostly July.

Type collection: "California, near the summit of Castle Peak [Mt. Sanford], Sierra County, at 9,000 feet, J. G. Lemmon."

38. RANUNCULUS ADONEUS A. Gray. Proc. Acad. Phila. **15**: 56. 1864.

Caudices 3–4 cm. long and 4–10 mm. in diameter, often as many as 9 in a cluster, closely and densely clothed with dead leaf bases; radical leaf blades finely divided, semi-circular to reniform in outline, 1–2 cm. long, 2–3 cm. broad, deeply parted, the primary divisions again twice-lobed into linear segments, proximally truncate or cordate and distally rounded, petioles 4–10 cm. long, stipular leaf bases 3–4 cm. long, persisting one or more seasons; cauline leaves alternate, about 2, the bracts dissected, sessile; petals when fully expanded 13–18 mm. long, 10–19 mm. broad; achene beak filiform, 1.2–1.5 mm. long, falcate-curving and often recurved.

Moist ground above timber line at 3,000–4,000 meters elevation; Northwestern Wyoming; occasional in the Wasatch and Uintah Mountains, Utah; Colorado. Arctic-alpine grassland. July and August.

Type collection: "No. 81 of last year's collection by Dr. Parry." Rocky Mountains in Colorado Territory, 1862.

38 A. RANUNCULUS ADONEUS var. **alpinus** (S. Wats.) L. Benson, comb. nov. *R. orthorhynchus* Hook. var. *alpinus* S. Wats. in King's Rep't. **5**: 9. 1871. *R. stenolobus* Rydb. Bull. Torrey Club **29**: 159. 1902.

Caudex 2–3.5 cm. long, flowering stems 15–30 cm. long, more branched than in the typical species; ultimate leaf divisions 1–2 mm. broad, the

stipular leaf base more frequently scarious than thick, 2–3.5 cm. long; petals when fully expanded 8–13 mm. long; achene beaks usually not recurved.

Near snow banks at 3000–3500 meters elevation; northwestern Wyoming and the Wasatch and Uintah Mountains, Utah. Arctic-alpine grassland. July and August.

Numerous Idaho and western Wyoming specimens connect this variety with *R. Eschscholtzii* var. *Suksdorfii.*

Type collections: (1) Var. *alpinus,* "The large form occurs in low lands in Washington Territory; the variety, in the Wahsatch Mountains, at an altitude of 10,000 feet; July." The TYPE is Wasatch Mountains, Utah, 40th Parallel, 10,000 (9,000 on some labels) feet, *S. Watson* in July, 1869. Confused with *R. orthorhynchus* probably because of the dissected leaves. (2) *R. stenolobus,* "WYOMING: Headwaters of Cliff Creek, 1900, *C. C. Curtis* (type in herb. N. Y. Bot. Gard.)."

39. RANUNCULUS NIVALIS L. Sp. Pl. 553. 1753. *R. nivalis* f. *subglobosus* Polunin, Bull. Nat. Mus. Can. (92) pt. 1: 215, *pl. 6. f. (b), upper left.* 1940.

Boggy tundra mostly near sea level or up to 800 meters elevation near Mt. McKinley, Alaska; circumboreal; Northern Alaska and along the shore and islands of the Arctic Ocean to Labrador; Greenland and Iceland. Arctic-alpine grassland and tundra. July and August.

A specimen from Capitol Peak, Colorado (*Penland 1512, CA*) is probably this species. According to Dr. Penland, none of the specimens have fruit. The glabrous receptacle agrees with *R. nivalis.* The plant shows some resemblance to *R. adoneus,* however.

Type collections: (1) *R. nivalis, "Habitat in alpibus Lapponiae, Helvetiae."* The following statement appears in Rees' Cyclopedia, volume 29 (pages not numbered; *Ranunculus* under "R"), "Found by Linnaeus in Lapland, by the alpine rivulets on the snowy mountains of that country. Martens had previously gathered it in Spitzbergen." (2) f. *subglobosus,* "Type in the British Museum: *Nicholas Polunin,* Wohlstenholme, Hudson Strait, No. 233, August 27, 1934."

40. RANUNCULUS SULPHUREUS Phipps, Voy. N. Pole 202. 1774. *R. altaicus* Laxm. Nov. Comm. Acad. Petrop. **18**: 533. 1774.

Tundra near sea level; circumboreal; Bering Straight and St. Paul Island, Alaska; Canadian Arctic Archipelago and the land adjacent; Gulf of St. Lawrence; Greenland; perhaps Iceland. Arctic-alpine grassland and tundra. Late June to early September.

Type collections: (1) *R. sulphureus.* The following is quoted from a letter from Dr. H. W. Rickett of the New York Botanical Garden: "No habitat or location given. But on p. 58 he mentions sending a party ashore on Low Island, off the coast of Spitzbergen, and quotes Dr. Irving thus: the ground was 'covered with moss, scurvy grass, sorrel, and a few ranunculuses then in flower.' Since this is the only mention of vegetation in the text, it is probable that *R. sulphureus* was collected then (July 29). The work on plants is often

but rather groundlessly attributed to Solander. On pp. 12–13 of Introduction, Phipps acknowledges his indebtedness to Banks 'for his assistance in drawing up the account of the productions of that country.' If Solander had had a hand, he would have mentioned it. If specimens exist they should be in Brit. Museum." (2) *R. altaicus.* The following is quoted from Dr. Rickett: "Exclude from description reference to Tab. VII., which is an error for Tab. VIII. After the detailed description is the following: 'Circa finem Junii in alpium nivosarum planitie muscosa florenum inveni.' And in the abstract on p. 49 of same volume he says 'in fissuris praedictarum alpium umbrosis habitans.' Laxman lived, and presumably collected, in Kolivan, near the present Novosibirsk in the province of Zapadni. The Altai range begins about here. Note also the following introductory remarks: 'In describendis plantis sibiricis pergens, nunnullas illarum tantum nunc botanicis offerre volui, quas in summis altaicorum montium aeterne nive tectorum cacuminibus legi, quaeque mihi maxime singulares visae sunt.' The type of *R. altaicus* would therefore come from alpine locations in the Altai mountains."

41. RANUNCULUS MACAULEYI A. Gray, Proc. Am. Acad. **15**: 45. 1879.

Meadows in the mountains at 3,400 to 3,800 meters elevation; Rocky Mountain System in Southwestern and South-Central Colorado and Northern New Mexico. Arctic-alpine grassland. July.

Type collection: "Rocky Mountains in San Juan Co., Colorado, Lieut. C. H. McCauley, Mr. F. N. Pease." "McCauley collected 2 specimens . . . in the summer of 1877."

42. RANUNCULUS GRAYI Britt. Bull. Torrey Club **18**: 265. 1891. *R. pedatifidus* Hook. Fl. Bor. Am. **1**: 18. *Pl. 8. f. B.* 1829, not J. E. Smith in 1819. *R. Hookeri* Regel, Reisen Ost-Sib. **1**: 47. 1861, not Schlect in 1834. *R. Drummondii* Greene, Erythea **2**: 192. 1894.

High peaks of the Rocky Mountains in Alberta (lat. 52°–55°, *Drummond*) and in Colorado (Gray's Peak, *Patterson* and at 13,000 feet elevation near Ironton, *S. H. Camp* in 1893.) The writer has seen only the Ironton specimen. Hooker's figure shows a plant with more deeply- and completely-dissected leaves and with sepals nearly as long as the petals. The apparent relationship is to *R. Eschscholtzii* Schlect. Arctic-alpine grassland. Summer.

Type collection: "Barren summits of the Rocky Mountains, on the eastern side of the ridge, lat. 52° to 55°, *Drummond.*" The later names are based on the same type.

43. RANUNCULUS PYGMAEUS Wahl. Fl. Lapp. 157. 1812.

Radical leaf blades simple, semicircular, 5–9 mm. long, 6–11 mm. broad, 3-parted or -divided, the middle lobe entire, the lateral 2–3-lobed, proximally truncate or nearly cordate and distally rounded in outline, petioles 1–3.5 cm. long, stipular leaf bases up to 1 cm. long; cauline leaves alternate or practically opposite, the bracts divided, sessile; achenes 40–50 in an ovoid or subglobose head 2.5–4 mm. long by 2.5–3 mm. in diameter.

Damp meadows and tundra at low elevations near the Arctic Sea and up to about 1,600 meters elevation in Alberta; circumboreal; Alaska to the Canadian Rockies; Ellesmereland to Labrador; Greenland; Spitzbergen. Arctic-alpine grassland. July to September.

43 A. RANUNCULUS PYGMAEUS VAR. PETIOLULATIS Fern. Rhodora **19**: 137. 1917.

Radical leaf blade divided, the divisions, sometimes shortly petiolulate, the middle division again 3-lobed, the lateral divisions 2- or 4-lobed or -cleft; head of fruits cylindrical, 5–7.5 mm. long and 3–4.5 mm. in diameter.

Damp, mossy hollows at 950–1,000 meters; Mt. Albert, Gaspe County, Quebec. Arctic-alpine grassland. August.

Type collection: "QUEBEC: damp mossy hollows in shade of amphibolite rocks, altitude 950–1000 m., Mt. Albert, Gaspe County, August 8 & 10, 1905, *Collins & Fernald*, no. 82 in large part (TYPE in Gray Herb.). . . . On Mt. Albert collections were made on two days at different points and all the material distributed under one number. The full sheet retained at the Gray Herbarium contains a few plants of true *R. pygmaeus*, but most of the specimens (presumably from a different station) are the variety."

44. RANUNCULUS RHOMBOIDEUS Goldie, Edinb. Jour. **6**: 329. 1822. (?) *Ranunculus ovalis* Raf. in Desv. Jour. Bot. **4**: 268. 1814, *nomen nudum*. *R. brevicaulis* Hook. Fl. Bor. Am. **1**: 13. 1829.

Prairies from Moose Jaw to Manitoba and Ontario and from the Dakotas to Michigan. Prairie grassland and northern coniferous and northeastern pine forests. March to May.

Type collections: (1) *R. ovalis*, "Canada." Many authors have attributed this name to *R. rhomboideus*, but there is little evidence that it was applied to that species, cf. Fern. Rhodora **38**: 175–7. 1936. (2) *R. rhomboideus*, "In dry sandy fields, near Lake Simcoe, Upper Canada [Ontario]." Collected by Goldie in Ontario County. (3) *R. brevicaulis*, "Shores of Lake Huron. *Dr. Richardson.* Drummond."

45. RANUNCULUS GLABERRIMUS Hook. Fl. Bor. Am. **1**: 12. *pl. 5. f. A.* 1829. *R. Austinae* Greene, Erythea **3**: 44. 1895.

Sandy soil in the sagebrush region at 300–1,700 meters elevation Northern Great Basin from British Columbia to Plumas County, California, and to Western Montana, and Western Colorado; Newell and Dickinson, South Dakota. Northern desert. April and May; the first flower of spring through much of its range. Both varieties are described in Abrams, Ill. Fl. Pac. Sts. vol. 2. (in press).

Type collections: (1) *R. glaberrimus*, "Common on the mountains around the Kettle Falls [Columbia River in Washington] and on the Rocky Mountains near the limits of perpetual snow. *Douglas.*" The Kettle Falls specimen is designated as a lectotype. (2) *R. Austinae*, "Crevices of lava rock east of Willow Creek Valley [Modoc County] in Northern California, Mrs. R. M. Austin, 1894. Species evidently allied to *R. glaberrimus*, though very distinct by its slender habit, snow-white petals, and elongated head of achenes." The petals of *R. glaberrimus*, like those of many other *Ranunculi*, turn white when they wither. The habit and head of achenes are normal for *R. glaberrimus*. A review of the Herbarium Greeneanum in 1935 failed to reveal the type specimen. ISOTYPES: *US 1466016, NY, UC.*

45 A. RANUNCULUS GLABERRIMUS VAR. ELLIPTICUS Greene, Fl. Fran. **1**: 298. 1892. *R. ellipticus* Greene, Pittonia **2**: 110. 1890. *R. Waldronii* Lunell, Am. Midl. Nat. **3**: 12. 1913.

Mountain meadows and the edge of the Great Plains at 1,500 to 3,000

meters elevation; from Lytton, British Columbia, through the Great Basin and Rocky Mountains to Truckee, California, western Montana, western South Dakota and Colorado; North Rim of the Grand Canyon, Arizona; Rio Arriba County, New Mexico. Western pine forest; plains grassland. April to June.

Type collections: (1) *R. ellipticus,* "Lower and Middle mountain districts of Colorado, Utah and Nevada to eastern California." Since there was only one California collection, the writer proposes it as a LECTOTYPE: Wet gravelly ground on road to Donner Lake [from Truckee] *C. F. Sonne,* May 16, 1886, *HGr 2583.* (2) *R. Waldronii,* "The type was collected on May 14. 1912, in a moist pasture at Dickinson, Stark County, in the southwestern part of this state [North Dakota] . . . named in honor of its first collector, Mr. Clarence H. Waldron. . . ." The TYPE was kindly sent to the University of Arizona for examination by Dr. C. O. Rosendahl of the University of Minnesota.

45 B. RANUNCULUS GLABERRIMUS var. RECONDITUS (Nels. & Macbr.) L. Benson, Am. Jour. Bot. **23**: 170. 1936. *R. triternatus* A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. reconditus* Nels. & Macbr. Bot. Gaz. **56**: 473. 1913.

Vernally moist slopes at 1,000–1,200 meters; Klickitat County, Washington, and near The Dalles, Oregon. Western pine forest (?). April and May.

Type collection: "Klickitat Co., Washington Terr., on high hills near Goldendale, *Howell,* by whom it has been distributed under the name of *R. Hookeri.*" April 20, 1882.

Significant specimens, cf. L. Benson, Am. Jour. Bot. **23**: 170. 1936.

46. RANUNCULUS VERTICELLATUS Eastw. Bot. Gaz. **33**: 144. *f. 3.* 1902.

Known only from the type collection at Cape Nome, Alaska (fide type specimen). Arctic-alpine grassland. Summer.

Type collection: ". . . collected at Nome City during the flowering season of 1900." "Plants collected by Dr. F. E. Blaisdell at Nome City, Alaska."

47. RANUNCULUS JOVIS A. Nels. Bull. Torrey Club **27**: 261. 1900. *R. digitatus* Hook. Kew. Jour. **3**: 124. *pl. 4.* 1851, not Gilib. in 1781, not Willd, in 1842. *R. oreogenes* Greene, Pl. Baker. **3**: 2. 1901.

Moist ground of mountain meadows and near snowdrifts at 1,900–3,000 meters elevation; Fremont County, Idaho; Havallah Mountains, Nevada; northwestern Wyoming; Wasatch Mountains, Utah; Cerro, Southern Colorado. Northern coniferous forest. April to July, depending upon latitude and altitude.

Type collections: (1) *R. digitatus,* "Hab. in Rocky Mountains, near Fort Hall. *Mr. Burke.*" (2) *R. Jovis,* "The type no. is 5817, collected on the Thunderer, Yellowstone Park, July 13, 1899, by Messrs. Elias Nelson & L. N. Goodding." (3) *R. oreogenes,* "at Cerro Summit above Cimarron, 7 June, no. 50," *C. F. Baker. HGr 2430.* The disposal of this species should be rechecked with the type.

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STUDIES IN THE GENTIANACEAE: GENTIANA, SECTION PNEUMONANTHE, SUBSECTION ANGUSTIFOLIAE

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(WITH ONE FIGURE)

The plants known popularly as Pine Barren gentians constitute a natural subsection of the genus *Gentiana*. This group is characterized by the narrow leaves, the usually solitary flowers and the long corolla-lobes which far exceed the plaits and are either spreading or reflexed. The subsectional name, *Angustifoliae*, apparently introduced by Small (1933) without Latin diagnosis, may now be formally described as: Subsectio *Angustifoliae* Small, sectionis *Pneumonanthe*, generis *Gentiana*, foliis linearibus, floribus fere solitariis, lobis corollae longis, sinus multo excedentibus, aut expandentibus aut reflexis. Other species of the section *Pneumonanthe* have broader leaves and the corolla either cylindrical or, if infundibuliform, with the lobes more or less erect, not widely spreading.

KEY TO SPECIES OF SUBSECTION ANGUSTIFOLIAE

A. Stamens and pistil usually equaling the tube of the corolla at time of anthesis; corolla blue (rarely pink or white) dotted with green on inside of tube; plants tall, 1.5–4 dm. high ..... 1. *G. porphyrio*

AA. Stamens and pistil one-half to two-thirds the length of the corolla tube at time of anthesis; corolla white dotted with green on inside of tube; plants relatively low, 1–3.6 dm. high, usually 2.5 dm. or less ..... 2. *G. pennelliana*

1. GENTIANA PORPHYRIO J. F. Gmelin, Syst. Nat. ed. 13. **2**: 462. 1791.

Gentiana purpurea Walter (not Linnaeus, 1753), Fl. Car. 109. 1788. No type is extant. The original description designates the corolla as infundibuliform, lively purple within, the stem simple and the leaves linear. Except for the color of the inside of the corolla, this diagnosis fits the common Pine Barren Gentian. The color discrepancy is troublesome, but there seem to be two possible explanations for that. Walter may have had a specimen of the pink variety which is now known from southeastern North Carolina, or he may have based his notes on an herbarium specimen which had faded from blue to purple, as frequently happens in dried material. In any case, there is no other species of gentian, known from the Carolinas today, which has an infundibuliform corolla, truly linear leaves and a simple stem. Further, regarding the color, both Elliott (Sketch Bot. S. C. & Ga., **1**: 341. 1821) and Darby (Bot. So. St. p. 436, 1791), clearly referring to the same plant as that under discussion, stated that the corolla is blue tinged with purple. Since Gmelin's *G. porphyrio* is simply a new name substituted for Walter's *G. purpurea* because of the earlier homonym of Linnaeus, application of the epithet *porphyrio* must rest on interpretation of Walter's species.

Gentiana angustifolia Michx., Fl. Bor.-Am. **1**: 177. 1803. Described from meadows of lower Carolina and said to have narrowly linear leaves.

Dasystephana porphyrio (J. F. Gmelin) Small, Fl. S. E. U. S., 931. 1903.

Gentiana Stoneana Fernald, Rhodora **41**: 555. pl. 579. 1939. The TYPE specimen, in the Gray Herbarium, is illustrated in Rhodora. It is from a

"siliceous and argillaceous thicket north of Factory Hill," Nansemond Co., Va., *Fernald and Long no. 9611*. Argument for this new name rests on the thesis that Walter's description, on which depends the application of *G. porphyrio* Gmelin, really applies to another species of which specimens are listed from Southampton Co., Va., Beaufort Co., S. C., and eastern N. C. Examination of this material indicates that the leaves are not linear, nor are the corollas truly infundibuliform. These plants belong to *G. parvifolia* (Nutt.) Britton, not to *G. purpurea* Walter. Although the flowers of the Pine Barren Gentian are distinctly funnelform, a fact attested by many authors, as Small (1933, p. 1052, 1054), Fernald wrote, "I find myself quite incapable of believing, when Walter described a plant with infundibuliform corolla lively purple within, that he referred to a plant with rotate azure- or indigo-blue flower." On this basis, Fernald renamed the species.

Slender perennial, 1.5–4 dm. high from a cluster of several fibrous roots which are 1–4 mm. thick; basal leaves narrowly elliptic, 1–4.5 cm. long, 6–7 mm. wide; cauline leaves linear, acute or obtuse, with the margins somewhat revolute, 0.7–6 cm. long, 1–4 mm. wide; flowers usually solitary and terminal, rarely two or three borne on pedicels in the axils of the upper leaves; calyx 2–3 cm. long, with the tube 0.8–1.2 cm. long and the lobes linear, acute, 0.8–2.3 cm. long; corolla funnelform, 3–5.5 cm. long with the tube 3.0–4 cm. long, greenish blue on the outside, blue spotted with green within; plaits lacerate, 3–6 mm. long, deep blue; lobes 1.0–1.5 cm. long, spreading or reflexed, deep blue, spotted with green below; stamens as long as the corolla tube; anthers yellow; pistil 2.5–3.5 cm. long; stigmatic lobes recurved, 2–5 mm. long. For an excellent description of the color of the flower, see the account by Pennell (1916).

Gentiana porphyrio is a plant of the Atlantic Coastal Plain, ranging from Monmouth County, New Jersey, to Florence, Florence County, South Carolina, and inland as far as Hartsville, Darlington County, South Carolina, Aberdeen, Scotland County, North Carolina and Fayetteville, Cumberland County, North Carolina. The characteristic habitat is in sandy pine barrens, where the plants may occur in situations ranging from the dry pine woods to moist peaty depressions. Data with one collection from near South Quay, Nansemond County, Virginia, indicate that the plants were growing there in hard gray clay.

Specimens seen:[1] Northernmost—pine woods, Monmouth Co., N. J., Torrey Herbarium (NY); easternmost—Manahawken, Ocean Co., N. J., *Bayard Long* (GH); westernmost—Hartsville, Darlington Co., S. C., *J. B. Norton 505* (US); southernmost—10 miles east of Florence, Florence Co., S. C., *A. N. Leeds 1622* (PH); oldest—Sept., 1814, Batsto, Burlington Co., N. J., ex herb. *F. J. Bumstead* (Corn); no. of collections seen—61.

The flowering time is earlier in the north and later in the south. From a study of data on herbarium sheets, extreme dates for flowering specimens in New Jersey are September 1 and October 28; in North Carolina, October 11 and December 15; and in South Carolina, October 25 and November 4. Probably flowers may be found in South Carolina much later than is indicated here, but at present few collections are available from that state.

[1] Names of herbaria are abbreviated as: (Corn) Dept. of Botany, Cornell University; (GH) Gray Herbarium, Harvard University; (NY) New York Botanical Garden; (Ph) Academy of Natural Sciences of Philadelphia; and (US) United States National Herbarium.

The most notable variation is in the color of the flowers. These vary from deep blue to pink. I have seen the pink phase in the garden of Mrs. J. N. Henry, Gladwyne, Pennsylvania. These plants came originally from near Wilmington, North Carolina.

Information on the cytology and breeding relationships of this species is still lacking. The chromosome number should be determined for plants from various parts of the range, also for both typical and pink-flowered specimens. Genetical studies should include experiments to determine the degree of compatability with *G. pennelliana*.

According to Pennell (1916) the oldest illustration was published in 1758, in Edwards' "Gleanings of Natural History, vol. 5, 1.98." An excellent colored plate appeared in Addisonia, vol. 1, 1916, plate 35.

2. GENTIANA PENNELLIANA Fernald, Rhodora **42**: 198. 1940.

Gentiana alba Croom (not Muhl. 1813), Am. Jour. Sci. **25**: 69. 1833.

Diploma tenuifolia Raf., Flora Telluriana **3**: 27. 1836. The TYPE, at the New York Botanical Garden, was collected in Florida, in 1832, by Mr. Croom.

Dasystephana tenuifolia (Raf.) Pennell, Bull. Torr. Bot. Club. **46**: 183. 1919.

Gentiana tenuifolia (Raf.) Fernald (not Petrie, 1913), Rhodora **41**: 557. 1939.

Slender perennial, 1–3.6 dm. high, from a cluster of several fibrous roots which are 1–4 mm. thick; leaves linear or narrowly elliptic-linear, acute or obtuse, revolute, 0.5–3 cm. long, 1–3 mm. wide; flowers usually solitary and terminal, rarely two or three borne on pedicels in the axils of the upper leaves; calyx 1.7–3 cm. long, with the tube 0.7–1.0 cm. long and the lobes linear, acute, 1–2 cm. long; corolla 4.5–6 cm. long with the tube 3.5–4.5 cm. long, white dotted with green on inside, greenish white on outside; plaits lacerate, 3–10 mm. long, white; lobes 1.2–1.8 cm. long, ovate-elliptic, spreading, white; stamens one-half to two-thirds the length of the corolla-tube at time of anthesis; pistil 2.5–2.7 cm. long; stigmatic lobes slightly spreading, 1 mm. long.

Gentiana pennelliana is a plant of very limited distribution on the East Gulf Coastal Plain in western Florida, ranging from Wakulla County westward to Walton County and northward to Gadsden County. The habitat usually is moist places in low pine woods.

Specimens seen: Northernmost—low pinelands near Wetumpka, Gadsden Co., *J. K. Small et al. 10987* (NY); easternmost—flatwoods, Newport, Wakulla Co., *H. Kurz* (NY); westernmost—Point Washington, Walton Co., *C. D. Mell* (US); southernmost—Apalachicola, Franklin Co., *Biltmore Herbarium 467b* (GH, NY); oldest—1832, Florida, *Croom* (NY); no. of collections seen—21.

The flowering time, as determined from the data on herbarium labels, extends from late October to January. No noteworthy variations in the color of the corolla are known. In the herbarium, the flowers may become brownish.

As interpreted by the descriptive taxonomist, *Gentiana porphyrio* and *G. pennelliana* are distinct species with both morphological and geographical discontinuity. Genetical discontinuity must yet be demonstrated.

Illustrations: see figure 1.

FIG. 1. *Gentiana pennelliana* Fernald. Specimens collected by Chapman in Florida. Sheet in U. S. National Herbarium, no. 59697.

SUMMARY

The Subsection *Angustifoliae* of *Gentiana*, Section *Pneumonanthe* contains two species which are distinguished by several characters. The proper name for the blue-flowered species is *Gentiana porphyrio*.

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Literature Cited

Pennell, F. W. 1916. *Dasystephana porphyrio.* Addisonia **1**: 69–70, plate 35.

Small, J. K. 1933. Manual of the southeastern flora. New York, The Science Press Printing Co., p. i–xxii, 1–1554.

NOTE:—Since the above was written, the writer has observed in the pine barrens of New Jersey white-flowered plants of *G. porphyrio*. Rumors are also current of the pink-flowered phase in New Jersey.

THE SUCCESSFUL REVIVAL OF NOSTOC COMMUNE FROM A HERBARIUM SPECIMEN EIGHTY-SEVEN YEARS OLD

CHARLES B. LIPMAN

The author's interest in the longevity of microorganisms as indicated by a number of published studies has led him to search for old materials of appropriate kinds from many sources. Among other sources which appealed to him as interesting and useful for obtaining material of no great age, and yet of significant age and authentic dating, was herbarium material from the cryptogamic collections. Through the great kindness of Doctor Francis Drouet of the Field Museum of Natural History, it was possible for me to obtain specimens of several algae from such a collection. These algae were inoculated into sterile Detmer's solution in Erlenmeyer flasks. The cotton stoppers were protected from dust by paper caps. In most cases the material taken from the herbarium sheets was very scanty and it consisted of desiccated fragments or scales. In the period of more than two years during which the cultures were maintained on a table in the laboratory, only one culture, namely one of *Nostoc commune* Vauch., developed growth of new masses of the organism as will be related below. During the incubation of the cultures the temperature conditions were not controlled, but varied from night to day, and from season to season as is characteristic of a laboratory at Berkeley. The extremes of temperature to which the cultures were subjected were approximately from 14° C. to 30° C. The light was mostly that of indirect sunlight from a south window, but in the winter months was supplemented by light from a 100-watt lamp during most of the day and night.

The specimen of *Nostoc* which was revived and produced vigorous new growth was derived from the collection of H. Royers, now a part of the collections of the Cryptogamic Herbarium of the Field Museum of Natural History. The label on the original specimen is as follows:

Nostoc commune Vauch
Germany: Zwischen Naumburg und den Sperlingsholze,
Preussen. 26 Juni 1853.
C. Schliephacke

From the material of this specimen donated by Dr. Drouet the first culture was prepared on the 1st April 1939. A small amount of the material was used in this culture, the balance being reserved for later inoculations. Growth was first noted in this culture on the 15th October 1939. This growth manifested itself by the appearance of dots of green on the original material and these green dots always showed bubbles of gas presumably oxygen from

photosynthesis. It is worthy of emphasis that it was always directly from the old material that the green dots and the gas bubbles arose. Microscopic examination showed typical cells and other structures of *Nostoc commune*. The long period of exposure of the original *Nostoc* material to the culture solution before growth developed is particularly noteworthy and seems to be characteristic as will be shown below. The result obtained with the first inoculation thus indicates that *Nostoc commune* may be revived after remaining in a desiccated state on a herbarium sheet for eighty-six years. This conclusion need not be allowed to rest on one observation alone, however, as the following discussion renders clear.

A second inoculation from the same source of *Nostoc* material was made on the 20th July 1939 with exactly the same technique as that employed in the first inoculation. In this culture the first growth noticed was on the 1st June 1940 or about ten months after the inoculation was made. Again the first evidence of growth manifested itself by the appearance of small dark green dots or tiny patches on the old material, and gas bubbles were easily discernible.

When the second culture developed growth, I decided to try a third inoculation. This was done on the 13th July 1940. On the 4th February 1941 growth was first noted in this culture. Microscopic examination in this as in the first and the second cultures showed typical *Nostoc commune* cells and chains of cells. This third culture proves moreover that the dried *Nostoc* material may withstand desiccation for eighty-seven as well as eighty-six years. How much longer such material can withstand desiccation and other untoward conditions on a herbarium sheet can of course only be ascertained by continued experiments of this kind with the original herbarium material as long as that can be spared.[1]

Of the other algal specimens tested by the same technique none have as yet shown signs of life. These algae included other and older specimens of *Nostoc* as well as other forms of blue-green and of green algae. In this regard, however, it is important to note that there is very little, if any, information at hand relative to the treatment which different specimens in the same herbarium received. For example, if fumigation or other methods of preservation had been employed, the specimens can hardly have survived in living form, unless the poisoning technique had been ineffective. It is doubtless true that some specimens of cryptogams had not been subjected to poisons at all, whereas others may have been treated drastically. In other words negative results such as those mentioned above remain under the

[1] Since this paper was sent to the printer, a fourth culture of *Nostoc*, made from the same herbarium specimen, has developed good growth after an incubation period of nearly five months. In addition, a culture of *Anabaena oscillarioides* from a specimen 74 years old has after an incubation of nearly two years just begun to show characteristic cells and chains of cells.

circumstances indecisive, relative to the longevity of the algae, whereas a positive result such as the one here reported for *Nostoc* is clearly decisive.

The writer's search of the literature does not reveal thus far any cases of greater longevity for algae than the one reported above. Certain seeds have, however, been shown to possess greater longevity. For example, the viability of *Nelumbium* seeds at the Kew Gardens after one hundred and fifty years, and of seeds of four or more orders in Paris after one hundred and fifty-eight years as reported by Becquerel are well known and decisive so far as they go.[2] The reports of Ohga regarding viability of seeds of *Nelumbium* from a peat bog in Manchuria after an estimated four hundred years of inactivity are also to the point but not decisive because of the uncertainty in the estimate of the age of these seeds. All these observations are in striking contrast to those which I have published on the longevity of bacteria, which appear, at least in some instances, to live indefinitely in a state of suspended animation. Of course, the observations on algae are still quite fragmentary and therefore do not make as satisfactory a comparison with those on bacteria as we should have. But the observations on seeds are in another category. They indicate quite strongly that seeds do not survive the ravages of time and untoward conditions nearly as well as bacteria. This subject, however, will be discussed more fully elsewhere. As regards the comparison of algal material and seeds, it may be remarked that the latter would seem to have the advantage over the former in resisting desiccation and other untoward conditions by reason of the protection to the embryo furnished by the seed. Such protection is especially great for example in the case of *Nelumbium*. The bits of algal material in a herbarium specimen on the contrary are completely exposed to the forces of the environment.

SUMMARY

Nostoc commune Vauch., from a herbarium specimen, has been revived and made to grow luxuriantly in culture solution eighty-six and eighty-seven years after it had been collected and placed in the herbarium.

THE UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

[2] See the excellent review by J. H. Turner, Kew Bull. 1933: 257–268.

BREEDING WORK TOWARD THE DEVELOPMENT OF A TIMBER TYPE OF BLIGHT-RESISTANT CHESTNUT: REPORT FOR 1940[1]

ARTHUR HARMOUNT GRAVES

(WITH ONE FIGURE)

The season of 1940 was the poorest for effective cross pollination of the chestnut that we have experienced since we began the work in 1930. The spring was abnormally cold, and continued so into the month of July.[2]

The cold weather had the following important effects:

1. Flowering was delayed. Usually, with some exceptions, all species and hybrids have finished blooming at the Hamden (Conn.) Plantation by July 15. (Of course, with the everblooming *Castanea Seguinii* and some of its hybrids, flowering often continues up to frost.) But in 1940 some Japanese-American and other hybrids were still in flower on August 1, and a few Chinese trees (*C. mollissima*) were still in their prime at this date.

2. The above statement applies to those flowers that matured. Apparently on account of the cold, some of the pollen bagged for crossing never matured, and many of the pistils bagged for crossing dropped off in the bags, both before and after pollination.

3. After crossing, fertilization did not result as regularly as usual. Many burs developed parthenocarpically, containing no embryos. It is possible that the unusual dryness of August and September played some part in this. We should bear in mind that only a comparatively short time is available for the chestnut to develop its fruit and ripen its seeds, as compared with the much longer period that oaks and hickories have.

POLLEN RECEIVED IN 1940

Pollen of the chestnut was received toward the end of June and in early July, from several institutions or persons whose cordial cooperation we take pleasure in acknowledging. Lack of space prevents us from including all their names in this report.[3]

[1] Brooklyn Botanic Garden Contributions, No. 95. For a statement of the purposes and a brief review of the work, see Bull. Torrey Club **67**: 773–77. 1940. Recent annual reports have been published in the Brooklyn Botanic Garden Record, as follows: for 1936, **26**: 47–60; for 1937, **27**: 44–55; for 1938, **28**: 52–60; for 1939, **29**: 58–63; for 1940, **30**: 87–92.

[2] The records at the U. S. Weather Bureau in New York City give the minimum temperature on July 4, 1940, as 58°. This was the same as the maximum temperature on December 25, 1940, namely, 58°; literally, as "cold as Christmas."

[3] The complete list of donors of pollen in 1940 appears in the Annual Report of the Brooklyn Botanic Garden for 1940, Brooklyn Bot. Gard. Record **30**: 88, 89.

The source of the pollen received from the Stark Bros. Nurseries, at Louisiana, Missouri, is of such general interest that we shall state it briefly here. In the settling of the estate of Mr. Luther Burbank, the Stark Bros. Nurseries took over various plant material there. But I shall let their letter speak for itself:

"When we took over the Burbank grounds there were about 500 chestnut trees in one row. They have since been cut down since Mrs. Burbank is using the ground. However, before taking them out we selected some of the most vigorous seedling trees and transferred them here to our grounds in Missouri. As a result we have about 10 trees here which are about 8 years old at this time. I have selected about 5 of these trees as the most vigorous in the lot and the catkins you received are from these trees. We will be interested in hearing of any results you obtain.

"Assuring you I am glad to be of service, I am

Sincerely yours,

(Signed) Glenn Thomas
Special Service Department
Stark Bros. Nurseries"

Earlier in the letter Mr. Thomas has this to say in response to a question on the pedigree of the trees bearing the pollen:

"I have been going through some of the records which we have here and I find that back in 1884 Mr. Burbank imported some Oriental chestnut seedlings from Japan and some European seedlings from Italy, and at the same time obtained some samples of chestnuts from the eastern United States and also some Chinquapins. According to the records these sorts were all hybridized back and forth in such a way that Mr. Burbank said all of his chestnuts had a most complicated ancestry. I find in the records that at first he was chiefly interested in getting from these crosses a hybrid which would produce a large, sweet nut, also a tree which would grow fast and bear young. Then when the chestnut blight became an important factor in the east Mr. Burbank's records indicated that he found 'hybrids of certain Oriental strains which appear immune to chestnut blight.' How he arrived at this conclusion I do not know, except that some of his hybrids may have been sent east for testing. I do not believe at this time there was any chestnut blight anywhere near California.

"Mr. Burbank's records state that he found crosses between the Oriental Chestnut trees from Japan and our native Chinquapins were the most resistant to chestnut blight. No doubt his later breeding experiments were concentrated on these crosses."

We made many crosses with this Burbank pollen, but the most important was a cross on our most resistant Japanese, from which we obtained 5 nuts.

HYBRIDS OF 1940

As a result of the season's work we harvested 401 nuts, as against 767 in 1939 and 930 in 1938. Twelve of the combinations from which we obtained

nuts are new to science, making a total of 48 new hybrid combinations made since we began this work in 1930.

Table 1 contains the list of the hybridizations in 1940 and the number of nuts resulting. All the hybridizing work was done on the trees on our own plantation at Hamden, Connecticut. As usual, the name of the female parent is given first. Those combinations which are new to science are preceded by an asterisk. The numbers at the left, in parentheses, correspond with the numbered notes which follow.

TABLE 1

Hybrids of 1940

		No. of Nuts
(1)	*Castanea crenata* × "Burbank"	15
(2)	*C. crenata* × *C. dentata*	47
	C. crenata × *C. floridana*	3
(3)	*C. crenata* × *C. pumila*	6
(4)	*C. crenata* × (*C* × *D*)[1]	15
(5)	*[*C. crenata* × (*C* × *D*)] × [(*C. mollissima* × *C. Seguinii*) × *C. crenata*]	1
(4)	(*C* × *D*) × *C. crenata*	8
	*(*C* × *D*) × *C. floridana*	1
(6)	(*C* × *D*) × (*C* × *D*)	39
(7)	*(*C* × *D*) × [(*C* × *D*) × *C. dentata*]	8
(8)	*(*C* × *D*) × [(*C* × *D*) × (*C* × *D*)]	51
(9)	*[(*C* × *D*) × (*C* × *D*)] × (*C* × *D*)	1
(10)	(*C. crenata* × *C. mollissima*) × *C. dentata*	19
	(*C. crenata* × *S8*[2]) × *C. dentata*	3
(11)	*C. dentata* × *C. crenata*	5
(12)	*C. dentata* × *C. mollissima*	10
(13)	*(*C. dentata* × *C. mollissima*) × (*C* × *D*)	2
(14)	(*C. dentata* × *S8*) × *C. crenata*	3
(15)	*(*C. dentata* × *S8*) × *C. mollissima*	32
(16)	*(*C. dentata* × *S8*) × (*C. crenata* × *S8*)	6
(17)	*(*C. dentata* × *S8*) × [(*C* × *D*) × *C. dentata*]	4
(18)	*C. mollissima* × *C. dentata*	32
(19)	*C. mollissima* × (*C* × *D*)	38
	(*C. mollissima* × *C. Seguinii*) × *C. dentata*	2
	(*C. mollissima* × *C. Seguinii*) × (*C. mollissima* × *C. Seguinii*)	20
	S8 × *C. mollissima*	1
	* *S8* × *C. neglecta*	3
(20)	(*S8* × *C. crenata*) × *C. dentata*	16
	*(*S8* × *C. crenata*) × *C. neglecta*	1
	(*S8* × *C. crenata*) × (*S8* × *C. crenata*)	3
	(*S8* × *C. crenata*) × (*C. crenata* × *S8*)	1
	*(*S8* × *C. dentata*) × (*C. mollissima* × *C. Seguinii*)	2
	C. Seguinii × *C. dentata* clone "Everbearing"	3
	Total	401

* *C* × *D* = *C. crenata* × *C. dentata*.

S8, one of the Van Fleet hybrids, is apparently a combination of *C. crenata* and *C. pumila*. The S8's in our plantation are from open pollinated seedlings of S8.

(1) This includes the cross with the Luther Burbank pollen mentioned in the text.

(2) We try each year to make more combinations of disease-resistant

Japanese and *dentata*. Most of the crosses this year we made on our Folk Japanese seedlings of 1930 (fig. 1), using *dentata* pollen sent us by Messrs. E. J. Grassman, from Elizabeth, N. J.; J. C. McDaniel, from Tennessee; Dr. G. A. Zimmerman, from Linglestown, Penn.; and Joseph St. John, from Monroe, N. Y.

(3) This cross was made with the purpose of finding out experimentally what is the composition of Dr. Van Fleet's hybrid "S8." This has generally been supposed to be the result of a cross of *C. crenata* and *C. pumila*. This year was the first time that *C. pumila* has bloomed at our plantation, the plants having grown from nuts sent us in the fall of 1935, by Mr. R. B. Clapper of the Division of Forest Pathology, from the U.S.D.A. nurseries at Bell, Maryland.

FIG. 1. *Castanea crenata*, 10 years old, and (according to results of inoculations) entirely disease resistant. Note low, bushy growth characteristic of the species, also good crop of large burs. Some of these are the result of crossing with the Burbank pollen.

(4) A cross of one of our Hammond Japanese-Americans (134 A 31) with our most disease-resistant Folk Japanese.

(5) This rather complicated cross represents two young hybrids (in brackets) which bloomed for the first time in 1940, at the age of three years.

(6) Represents a continued effort to get a good supply of F 2's by crossing together many Japanese-Americans.

(7) The pollen parent in this combination has grown from one of the first nuts we secured from crossing our Japanese-Americans. The first of these bloomed in 1934, at the age of three years. This was crossed with *dentata* pollen, received from the Division of Forest Pathology, U.S.D.A., at Washington, D. C. One of the trees resulting from this cross, namely, the pollen parent referred to above, bloomed this year at the age of six years, but with only staminate flowers.[4] These were used to pollinate one of our good Japanese-American hybrids—a cross of a Japanese owned by the late

[4] For a photograph of this hybrid, see Brooklyn Bot. Gard. Record 30: 65. 1941.

Mr. Beekman Winthrop, of Old Westbury, Long Island, and *C. dentata* from Washington, D. C., made by us in 1931. The resulting nuts from this cross represent a new combination.

(8) The same Winthrop Japanese-American crossed with pollen from an F 2 Japanese-American, resulting from a cross of two Smith Japanese-Americans in 1936 and blooming this year for the first time. This cross gave a particularly fruitful yield—about ⅛th of our entire crop.

(9) The reciprocal of the last, but here the pistil parent was young (3 years) and only one nut resulted.

(10) The pistil parent here is habitually a very late bloomer, given to us by the Division of Forest Pathology, U.S.D.A., in 1932. Pollen of *dentata* from wild trees was sent to us by Mr. Philip Smith, of Pawling, N. Y., arriving as late as July 19, in most years too late to be of service. But in this unusually late season this Japanese-Chinese hybrid was in its prime at this date; hence the cross produced a good yield.

(11) The *dentata* parent is the same as that mentioned in my report for 1939.[5] This year, obviously very nearly at the end of its life, it had many pistillate flowers which were crossed with our most resistant Japanese, but only five nuts were gathered.

(12) As was done last year, the American parent just mentioned (note 11) was crossed with our most resistant Chinese.

(13) The pistil parent is the result of a cross of wild *dentata* trees at Half Hollow Hills, in the township of Huntington, Long Island, N. Y., using pollen of *C. mollissima* sent from our Hamden plantation in 1935. It was part of an effort made that year to see if by using as the female parent the American chestnut, instead of the Japanese or Chinese, as we had always done before, any difference in the character of the offspring would result. As far as we can determine, the character of the female parent makes no difference in this cross. The *dentata* stock is incompletely dominant in both cases. The American-Chinese hybrid was, therefore, five years old in 1940 and was crossed with one of our best Japanese-Americans, the latter being the result of a cross of a Japanese chestnut on the estate of Mr. John Minturn, Oyster Bay Cove, Long Island, with *dentata* pollen. That Japanese tree is still in fine condition and is one of the best now living in the region of New York City. Only two nuts were secured from the cross this year, but since the cross includes so many good elements it will be tried again next year.

(14) The pistil parent is the result of a cross on the native chestnut shoots at Half Hollow Hills, Huntington, L. I., in 1935, using S8 pollen from our plantation. The hybrid was crossed this year with pollen from one of our best Japanese trees; for we have learned that the S8's in our plantation, although precocious and prolific, are not as disease resistant as could be desired.

(15) Another *dentata* × *S8* resulting from a Long Island cross (see notes 14 and 13, also report for 1935[6]). This hybrid bloomed for the first time in 1938. This year it was crossed with one of our best mollissimas, with splendid results. The nuts have a promising pedigree.

(16) Another *dentata* × *S8*, with a history like that of the preceding, crossed with a 1935 hybrid of a good Japanese and *S8*. The Japanese grew

[5] Bull. Torrey Club **67:** 775, note 5.

[6] See Brooklyn Bot. Gard. Record **25:** 66, 67.

from a nut obtained from the vicinity of Kyoto, Japan, through Dr. G. M. Reed, of the Brooklyn Botanic Garden, in December, 1931.[7]

(17) A fourth *dentata* × *S8*, with a history similar to that of the preceding three—this one crossed with the hybrid resulting from the back cross of Japanese-American with *dentata*, described in note 7.

(18) Resistant *mollissima* crossed with some *dentata* pollen sent us by Dr. G. A. Zimmerman, from Linglestown, Penn., through Miss Hilda Vilkomerson, and also by Mr. Joseph St. John, from Monroe, N. Y.

(19) This represents a continued effort to incorporate more of the resistance of the mollissima stock with the Japanese-American hybrids.

(20) *S8* × *C. crenata* contains no *dentata* in its constitution. It is fairly disease resistant; hence this cross with *C. dentata*. The *dentata* pollen used came from Elizabeth, N. J., sent by Mr. E. J. Grassman.

COOPERATIVE PLANTINGS

Because our own available land at Hamden, Connecticut is now fairly well stocked with species and hybrids, we are extending our plan of establishing cooperative plantations on land of responsible persons interested in bringing back the chestnut tree to North America. The trees growing in the first three of these cooperative plantations are listed in our 1939 report, but plantations are now too numerous even to name here. During 1940 we distributed more than 1500 seedlings in New Hampshire, Massachusetts, Connecticut, New York State, and New Jersey. In cases where particularly valuable hybrids have been distributed, the owners are required to sign the following statement:

> The undersigned agrees to grow this material for test purposes only, and further agrees not to propagate, sell, give away, or otherwise distribute the material until authorized to do so by Arthur H. Graves, Brooklyn Botanic Garden, Brooklyn, N. Y.

The area planted to trees is thus increased many times, so that the total number of trees growing is far larger than we could handle on our own plantation. As all plant breeders know, large numbers increase the chances of success, when a definite object is to be realized through breeding. Further, by this method of extension plantation, the trees are tested in a variety of soils and sites which we alone could not furnish.

VARIATION IN CASTANEA DENTATA

The chestnut, as a genus, shows a considerable amount of variability, and this character is shared by the different species.[8] For example, in the Amer-

[7] Brooklyn Bot. Gard. Record 25: 68, notes 11, 12.

[8] Darwin, Francis. The foundations of the origin of species, two essays written in 1842 and 1844, by Charles Darwin. p. 83, Univ. Press, Cambridge, 1909. "In many species the variability of certain organs or qualities is even stated as one of the specific characters."

ican chestnut, the qualities of the nuts varied so much that local forms received special names.[9] The European chestnut (*C. sativa*) and the Japanese (*C. crenata*) also show a wide variation in the size and quality of the nuts.

In the summer of 1918, when we made a survey of the American chestnut trees then growing in the New York City region, a large amount of variation was shown in the amount of disease resistance manifested by different individuals,[10] another evidence of the variability of the species.

Now we are confronted with a situation extending over the whole range of the native chestnut tree, characterized by a succession of young shoots arising from the stumps (or bases) of diseased and dead trunks. These shoots develop for a few years, but are at length penetrated by the blight fungus. This condition is due to the fact, as we have learned,[11] that the roots of the trees are more resistant to the attacks of the fungus than is the trunk or its branches.

This continued development of a very large number of new shoots from adventitious buds offers abundant opportunity for bud variation to occur. I believe that such variation should occur with greater frequency, or intensity, or both, in these basal shoots than in the ordinary branches developing from normal buds. However, there seems to be scant evidence in the literature in support of this belief, perhaps because of the unusual nature of the situation. Beyerinck,[12] however, as a result of pruning *Cytisus Adami*, obtained segregation in the shoots developing from dormant buds, showing an unstable chromosomal condition resulting from such treatment. The killing of chestnut trees to the base by the blight fungus and the subsequent development of shoots from adventitious buds seems to be a similar situation. In any case, however, this continued production of basal shoots in all probability entails a certain amount of bud variation, for this phenomenon is likely to occur even under normal circumstances; and it is entirely probable that some of this bud variation will be along the line of greater disease resistance. The fact that many of these young chestnut shoots seem to be living longer and getting larger than formerly may be due to just this situation, i.e., to bud variation in the direction of disease resistance.

Now, it is fortunate that many of these basal shoots live long enough to flower and bear nuts. The qualities developed through bud variation, if they are hereditary, may be represented in these embryos.

It is on account of the above reasoning that we are trying to obtain as

[9] Corsa, W. P. Nut Culture in the United States. U.S.D.A. Div. of Pathology, unnumbered bull., 1896. p. 88.

[10] Graves, A. H. Resistance of the American chestnut to the bark disease. Science **48**: 652, 653. 1918.

[11] Graves, A. H. The cause of the persistent development of basal shoots from blighted chestnut trees. Phytopathology **16**: 615–621. 1926.

[12] De Vries, Hugo. The mutation theory, Vol. II, p. 626. 1910.

many nuts as possible of wild American trees or shoots of *C. dentata*. At present we have growing on our plantation at Hamden, Connecticut, more than 100 young trees of *Castanea dentata*. These Americans have been grown during the past fifteen years from nuts obtained from many of the states where *Castanea dentata* is native. They are being tested for disease resistance. If the results are favorable they will be used for breeding stock. Last fall we received nuts from interested persons in the following States: Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, and Kentucky.[13]

We find that the best method of handling the nuts is to plant them immediately after gathering. If any nuts are to be mailed to us, they should be wrapped in damp sphagnum moss, moist cotton, or paper napkins, to prevent drying out. A few days in a heated room may be fatal, for drying kills the embyro. Any nuts sent us will be planted immediately in our cold frames at the Garden and labelled with the name of the sender and the locality of the parent tree. Address: Arthur H. Graves, 1000 Washington Avenue, Brooklyn, New York.

Acknowledgment. We are glad to have this opportunity to express our indebtedness to the many individuals and institutions, and especially to the Division of Forest Pathology, U.S.D.A., for their cordial cooperation with us in our project.

BROOKLYN BOTANIC GARDEN
BROOKLYN, NEW YORK

[13] See Brooklyn Bot. Gard. Record **30**: 91, 92. 1941.

MISCELLANEOUS TAXONOMIC NOTES

HAROLD N. MOLDENKE

Continued routine identification work in the herbarium of the New York Botanical Garden has revealed the desirability of a number of transfers from the genus *Polygonum* to the genus *Reynoutria* (formerly known under the name of *Pleuropterus*) and has brought to light two as yet undescribed species of *Peiranisia* and *Byrsonima* from Cuba.

Reynoutria Auberti (L. Henry) Moldenke, comb. nov. *Polygonum Auberti* L. Henry, Rev. Hort. **1907**: 82–83. 1907.

Reynoutria baldschuanica (Regel) Moldenke, comb. nov. *Polygonum baldschuanicum* Regel, Act. Hort. Petrop. **8**: 684, *pl. 10*. 1884.

Reynoutria campanulata (Hook. f.) Moldenke, comb. nov. *Polygonum campanulatum* Hook. f., Fl. Brit. Ind. **5**: 51. 1886.

Reynoutria ciliinervis (Nakai) Moldenke, comb. nov. *Polygonum ciliinervis* Nakai in Fedde, Repert. **13**: 267–268. 1914.

Reynoutria japonica var. **compacta** (Hook. f.) Moldenke, comb. nov. *Polygonum compactum* Hook. f. in Curtis, Bot. Mag. **106**: *pl. 6476*. 1880.

Reynoutria japonica var. **spectabilis** (de Noter) Moldenke, comb. nov. *Polygonum cuspidatum* var. *spectabile* de Noter, Rev. Hort. Belg. **35**: 232–234. 1909.

Reynoutria lichiangensis (W. W. Sm.) Moldenke, comb. nov. *Polygonum lichiangense* W. W. Sm., Notes Bot. Gard. Edinb. **8**: 197. 1914.

Reynoutria multiflora (Thunb.) Moldenke, comb. nov. *Polygonum multiflorum* Thunb., Fl. Jap. **1**: 169. 1784.

Reynoutria polystachya (Wall.) Moldenke, comb. nov. *Polygonum polystachyum* Wall., Numer. List 46, no. 1686, hyponym (1829), Pl. As. Rar. **3**: 61. 1832.

Reynoutria Spaethii (Damm.) Moldenke, comb. nov. *Polygonum Spaethii* Damm., Notizbl. Bot. Gart. Berlin **2**: 378. 1899.

Reynoutria Weyrichii (F. Schmidt) Moldenke, comb. nov. *Polygonum Weyrichii* F. Schmidt in Maxim., Prim. Fl. Amur. 234. 1859.

Peiranisia Bucherae Moldenke, sp. nov. Frutex vel arbor; ramulis gracilibus minute puberulis glabrescentibus; nodis valde abbreviatis; foliolis 6 vel 8 coriaceis utrinque pernitidis ellipticis, ad apicem rotundatis emarginatis, ad basim acutis, integris revolutis utrinque glabris vel parce pilosulis; glandulis 3.

Shrub or tree; branchlets slender, gray, minutely puberulent when young, soon glabrescent; nodes greatly abbreviated; leaf-scars large, horizontally oblong, with prominent margins; leaves alternate, evenly pinnate-compound with 3 or 4 pairs of leaflets; leaflets coriaceous, rather grayish green and very shiny on both surfaces, elliptic, 1.2–3.9 cm. long, 0.5–1.7 cm. wide, rounded and emarginate at apex, acute at base, entire and revolute along the margins, glabrous on both surfaces or with few scattered pilosulous hairs at the base; petiolules stout, about 1 mm. long, glabrous or very obscurely pilosulous-puberulent; gland circular, about 1 mm. in diameter, one between each of the 3 upper pairs of leaflets; rachis angular-costate, glabrous or very obscurely and minutely scattered-pilosulous; pedicels slender, 2.5–3 cm. long, very sparsely scattered-pilosulous with minute hairs; sepals

5, heavy, unequal, suborbicular, 3–6 mm. long and wide, rounded at both ends, venose, glabrous or the smaller ones microscopically pilose; petals yellow, large, irregular, unequal, 9–13 mm. long, 5–9 mm. wide, very venose, glabrous, the margins crisped; stamens 10, beakless; filaments about 1.4 mm. long, glabrous; anthers oblong, about 3 mm. long and 1.4 mm. wide; ovary elongate, flattened, 6 mm. long or longer, appressed-sericeous; immature legume flattened, elongate, 4 cm. long, with a minute circular disk on the very apex of the narrowed point, the valves thick-margined, glabrate.

CUBA—ORIENTE: Moa, *Mrs. George Conrad Bucher 78*, TYPE; in the Britton Herbarium at the New York Botanical Garden. The specimen was examined by my good friend, E. P. Killip, who was not able to place it in any known Cuban species.

Byrsonima Bucherae Moldenke, sp. nov. Frutex; ramis ramulisque appresso-tomentellis glabrescentibus; nodis valde annulatis subarticulatis; hornotinis densissime ferrugineo-tomentellis; petiolis crassiusculis dense ferrugineo-tomentellis canescentibus; laminis coriaceis, supra nitidis, anguste ellipticis vel elliptico-lanceolatis, ad apicem angustatis emarginatis, ad basim acutis vel obtusis, integris revolutis, subtus dense ferrugineo-farinaceis.

Shrub; branches and branchlets slender, gray, very closely appressed-tomentellous, glabrescent in age; nodes conspicuously annulate, subarticulate; twigs very densely ferruginous-tomentellous when young; leaves decussate-opposite; petioles stoutish, flattened above, densely ferruginous-tomentellous, the tomentum more appressed, incanous, and less obvious in age; blades coriaceous, gray-green and shiny above, ferruginous or brunneous beneath, narrow-elliptic or elliptic-lanceolate, 2.4–5.8 cm. long, 0.6–2.1 cm. wide, regularly narrowed to a narrow and slightly emarginate apex, acute or obtuse at base, entire and revolute along the margins, ferruginous-farinaceous above when immature, glabrate or subglabrate when mature, very densely ferruginous- or brunneous-farinaceous beneath; midrib slender, deeply impressed above, very prominent beneath; secondaries slender, 4–8 per side, short, divergent, conspicuously arcuately joined some distance from the margins, impressed above, sharply prominent beneath; veinlet reticulation abundant, impressed above, prominulous beneath; pedicels slender, about 2 cm. long, longitudinally costate, very densely ferruginous-tomentellous; receptacle long-villous; sepals ovate, densely ferruginous-tomentellous, the acuminate free portion recurved and revolute, with a pair of oblong basal glands about 1.5 mm. long at the base; petals 5, long-clawed, the stalk about 3 mm. long, glabrous, canaliculate above, the blade obcordate, about 5 mm. long and 5.1 mm. wide, irregular-margined; stamens 10, erect, close together; filaments about 2.5 mm. long, glabrous; anthers 2-celled, oblong, about 0.7 mm. long, the connective prolonged into a spur-like projection about 1–1.3 mm. long, glabrous; pistil 1; ovary ovate, about 1.7 mm. long, glabrous; styles 2, about 3 mm. long, glabrate.

CUBA—ORIENTE: Moa, *Mrs. George Conrad Bucher 57*, summer of 1939; in the Britton Herbarium at the New York Botanical Garden; named in honor of the collector. My good friend, C. V. Morton, recognized expert on this group, says of it "*Byrsonima* prob. sp. nov. aff. *B. Wrightiana* Urb. & Ndzu."

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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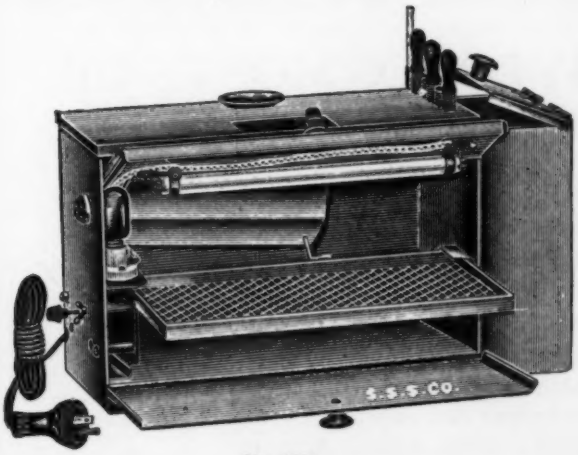

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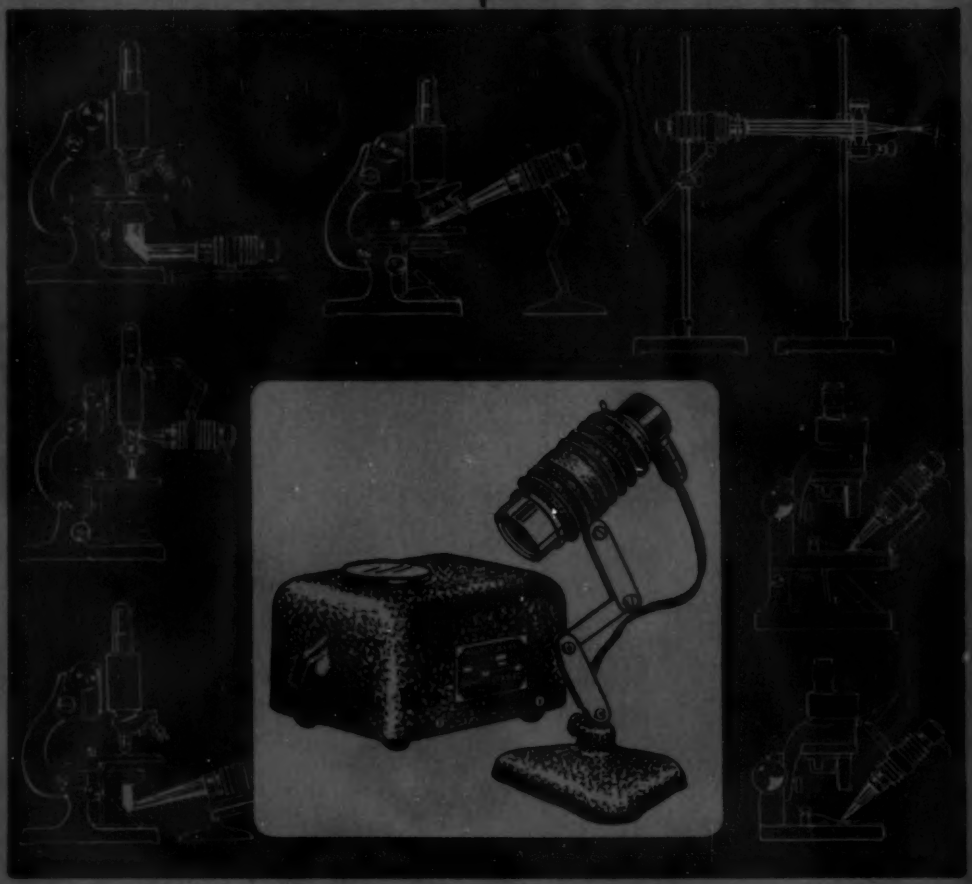

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